

EXPERIMENTAL PHYSIOLOGY

E. SHARPEY-SCHAFER

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Experimental Physiology

BY

SIR EDWARD SHARPEY-SCHAFER, F.R.S.

PROFESSOR OF PHYSIOLOGY IN EDINBURGH

FOURTH EDITION

WITH NINETY-TWO ILLUSTRATIONS

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P R E F A C E

THIS book contains precise directions for performing most of the fundamental experiments in Physiology, except those of a chemical nature. Most of the experiments described can be carried out by the student himself, working either in class or separately, but some—at least in this country—can only take the form of demonstrations. A certain number are intended for advanced students, although no attempt has been made to mark these off from the rest. Such selection can best be made by the teacher of the subject, and would be regulated by the requirements of his students and the nature of the examinations for which they are working.

I am indebted to my Assistants, Dr ERIC PONDER, Miss MAY L. WALKER, and Dr HENRY DRYERRE, for suggested additions as well as for emendations in some of the directions. Mr E. H. CAMERON has also kindly aided in the description of methods employed in the observation of entoptic phenomena.

UNIVERSITY, EDINBURGH,

October 1927.

ENGLISH MEASURES EXPRESSED IN THE METRIC SYSTEM.

WEIGHT (Avoirdupois).

- 1 grain = 0.0648 gramme.
 1 oz. = 28.350 grammes.
 1 lb. = 453.590 „
 1 cwt. = 51 kilogrammes.

LENGTH.

- 1 inch = 25.40 millimetres.
 1 foot = 30.48 centimetres.
 1 yard = 0.914 metre.
 1 mile (1,760 yards) = 1.6 kilometres.

VOLUME.

- 1 cubic inch = 16.387 cubic centimetres.
 1 cubic foot = 28.317 litres.
 1 pint = 568 cubic centimetres.
 1 gallon = 4.546 litres.

UNITS OF THE METRIC SYSTEM EXPRESSED AS ENGLISH MEASURES.

WEIGHT.

- 1 milligramme = 0.0154 grain
 (about $\frac{1}{65}$ gr.).
 1 gramme (weight of 1 cubic centimetre of water at 4° C.) = 15.432 grains.
 1 kilogramme (1,000 grammes) = 2.2 lbs.

LENGTH.

- 1 millimetre = 0.03937 inch (about $\frac{1}{25}$ inch).
 1 centimetre = 0.3937 inch (about $\frac{2}{5}$ inch).
 1 decimetre = nearly 4 inches.
 1 metre = 39.37 inches.

VOLUME.

- 1 cubic centimetre = 0.061 cubic inch (about 15½ minims).
 1 litre or cubic decimetre (1,000 c.c.) = 1.76 pints.

RELATION OF CENTIGRADE TO FAHRENHEIT THERMOMETERS.

Freezing Point	-	-	-	0° C.	32° F.
Boiling Point	-	-	-	100° C.	212° F.

1° Centigrade = 1.8° Fahrenheit.

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EXPERIMENTAL PHYSIOLOGY

PRELIMINARY

As a preliminary to any course of Experimental Physiology, the following dissections should be made :—

Frog.—In this the following parts are to be displayed :—

- (a) The brain (see Fig. 84) and spinal cord, with the nerves passing off from them.
- (b) The heart, with the main vessels leading to and from it (see Figs. 57, 58, 59, and 65).
- (c) The lungs.
- (d) The abdominal viscera, including stomach, small intestine, large intestine, liver, spleen, kidneys, bladder, and reproductive glands (see Fig. 27).
- (e) The nerves and muscles of the leg (see Figs. 28 and 29).

Rabbit.

- (a) The skull to be opened, and the several parts of the brain examined.
- (b) The trachea and the blood-vessels and nerves on either side of it to be displayed, and to be followed as far as possible both upwards towards the head and downwards into the thorax.
- (c) The contents and boundaries of the thorax to be examined. The several parts of the heart to be observed and the vessels which are connected with it. After removing the contents of the thorax, the sympathetic ganglia and the nerves (splanchnic) leading downwards from them towards the abdomen should be noticed.
- (d) The abdominal and pelvic viscera to be displayed.
- (e) The nerves and muscles of one of the hind limbs to be dissected.

Since these dissections form a part of every course of Biology, the student will probably already be familiar with them. If not, they should be made now.

CHAPTER I

Amœboid and Ciliary Movement

The fresh-water amœba.—Find an amœba in a drop of pond water under the microscope, and study its movements.

Amœboid movements and other changes in leucocytes.—Observe in a preparation of frog's blood the changes which the leucocytes undergo. The blood of certain crustacea, such as the fresh-water cray-fish, is even more instructive than that of the frog.

Ciliary movement.—(1) Gently scrape some epithelium from the roof of a frog's mouth, and shake the scrapings in a drop of normal salt solution or of Ringer's solution.¹ Observe with the microscope the ciliated cells and the movements of their cilia.

(2) Take a small fragment of the gills of a sea-mussel and examine it under the microscope in a drop of sea water. The cilia are much larger than those of the frog, and their movements more easily watched, especially when they become slow.

Experiments illustrative of protoplasmic phenomena.—The following experiments show that phenomena resembling those of cell-protoplasm can be produced by purely physical and chemical changes in unorganised materials.

1. Take on a glass rod a drop of ordinary olive oil which has been

¹ *Normal salt solution* contains 6 grammes NaCl to the litre of distilled water for the frog; 7 to 9 grammes NaCl for mammals.

Ringer's fluid is normal salt solution containing, in addition to NaCl, small amounts of sodium carbonate, calcium chloride, and potassium chloride. The method of making it recommended by Ringer was as follows:—

To each litre of normal salt solution add 10 c.c. of a one per cent. solution NaHCO_3 ; 10 c.c. of a one per cent. solution CaCl_2 and 7.5 c.c. of a one per cent. solution KCl.

A Ringer's fluid adapted for mammalian tissues is made by Locke's formula as follows:—

1000.00 c.c.	H_2O (distilled)
9.20 g.	NaCl
0.15 g.	NaHCO_3
0.24 g.	CaCl_2
0.42 g.	KCl

To the above, when employed as a perfusion fluid for the mammalian heart, 1 gramme pure glucose is added just before use.

coloured with Scharlach R., and place it gently on the surface of a 0.1 per cent. solution of sodium carbonate. Sketch the amœba-like changes of shape which it undergoes. With stronger solutions of sodium carbonate the drop of oil becomes rapidly vacuolated and tends to break up in an explosive manner.

2. A globule of mercury is placed in a watch-glass of dilute nitric acid (1 per cent.). (a) Introduce into the fluid near, but not touching, the drop a small crystal of potassium bichromate or (b) touch the globule with a steel needle. Observe the movements of the mercury.

3. **Rhumbler's experiment.**—Take a small piece of glass, such as a glass bead, which has been coated with shellac, and allow it to come into contact with chloroform placed in a watch-glass. The bead will be taken in (ingested) by the chloroform, but as soon as the shellac covering is dissolved, the glass will be ejected (excreted).

Experiments on ciliary movement.—1. In a model consisting of a thick rubber ball from which a flattened, curved rubber tube projects, notice that the tube straightens out or curves over to one side according to the tension of the contents of the ball. This movement, which resembles that of a cilium, is thus produced by variations in tension within the system.

2. In a frog which has just been killed, cut through the attachments of the lower jaw and carry the incision down the œsophagus to the stomach. Cut this organ across, seize the cardiac end with forceps, and dissect out the œsophagus together with the pharynx and a part of the mucous membrane of the mouth. Pin out the œsophagus and pharynx and adjacent parts of the buccal membrane on a flat cork with the inner surface uppermost. Rinse with Ringer's solution. Sprinkle a few grains of charcoal over the buccal end of the preparation, and notice that the charcoal is carried down as far as the stomach by the action of the cilia. In the same way, pieces of cork or wax, or even small flat pieces of heavy materials such as lead, may be passed over the surface.

3. **Effect of temperature on ciliary movement.** Fasten with pins two pieces of thread one centimetre apart across the above preparation of œsophagus, and slightly raised above it. Rinse the membrane with *ice-cold* Ringer solution. Drop a grain of charcoal on the buccal end, and, with a watch, record the number of seconds which the charcoal takes to pass over the interval between the threads. Again rinse the membrane, but this time with *warm* Ringer (25° C.), and repeat the experiment. Note the difference in time taken to traverse the space marked off by the threads. Lastly, rinse with Ringer heated to 50° C., and repeat the experiment. The ciliated cells are killed at this temperature, and the charcoal is no longer carried along.

CHAPTER II

The Electrical Apparatus in Common Use in Physiological Work

A **VOLTAIC** element or cell consists, in its simplest form, of two metals, *e.g.*, zinc and copper, or of zinc and carbon, immersed in a suitable fluid such as dilute sulphuric acid; the movements of ions which occur

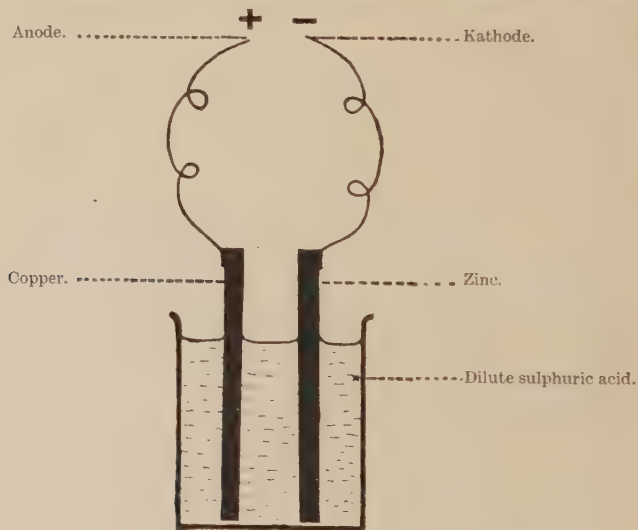


FIG. 1.—Voltaic couple.

under these circumstances in the fluid produce a disturbance of electrical equilibrium which manifests itself as a difference of electrical potential or pressure at the metals. If wires are attached to the parts of these outside the fluid it is found that the end of the wire connected with the copper is charged with positive electricity, and that connected with the zinc is charged with negative electricity; these ends are called the positive pole, or *anode*, and the negative pole, or *kathode*, respectively. The anode is said to be in a condition of higher potential and the kathode in one of lower potential, and when they are

joined electrical equilibrium tends to re-establish itself in the circuit thus closed. It is common to speak of a current as flowing from the anode to the kathode outside the cell and from the zinc to the copper inside.¹ The amount of this current depends upon the difference of potential produced within the cell. This is diminished by any increase of resistance to the flow of electricity, whether occurring within the cell or in the outside circuit. Electromotive force (E.M.F.) is measured in volts; thus the E.M.F. of a Daniell cell is 1·079 volts. It may be increased by coupling two or more cells together in series, the zinc of one connected with the copper of the next, and so on. When cells are coupled together, they form what is known as a *voltaic or galvanic battery*.

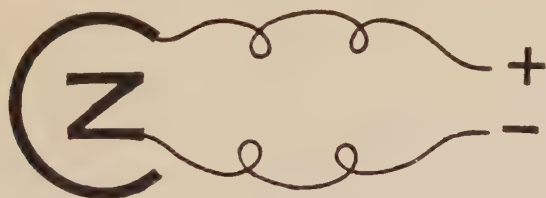


FIG. 2.—Diagram of a voltaic couple. Z, Zinc; C, Copper.

If electricity is generated simply by immersing plates of zinc and copper into acid the chemical action which ensues causes bubbles of hydrogen gas to form on the copper, and this not only introduces a resistance to the flow of current through the cell, but the hydrogen tends to set up a current (polarisation current) in the opposite direction in the cell and circuit; from both these causes the original E.M.F. of the cell becomes rapidly weakened.

To obviate this effect Daniell placed the copper plate in a saturated solution of copper sulphate and introduced a porous pot to separate this from the dilute sulphuric acid in which the zinc is immersed (Fig. 3). The zinc then dissolves in the acid, displacing hydrogen;² the hydrogen in its turn displaces copper from the copper sulphate, and the displaced copper is deposited on the copper plate, so that no bubbles of hydrogen are formed upon the metal, and if the copper sulphate solution is kept saturated, the E.M.F. of the cell remains constant. Commercial zinc, which is never pure, must always be

¹ Within the cell the electrical potential is highest at the zinc, which is therefore here the anode, and lowest at the copper, which is here the kathode.

² A solution of zinc sulphate being formed. It is convenient to use a saturated solution of zinc sulphate in the porous pot in substitution for the dilute sulphuric acid.

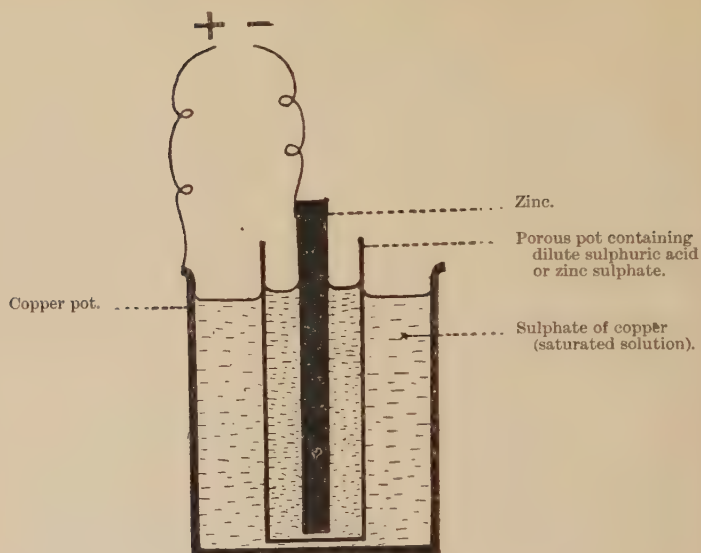


FIG. 3.—Daniell cell.

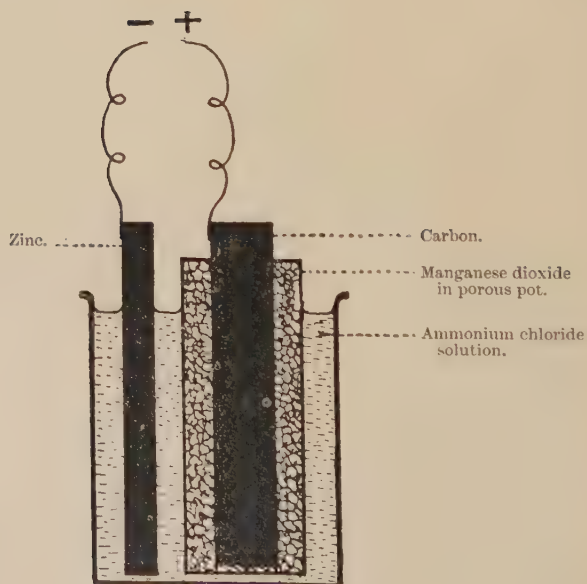


FIG. 4.—Leclanché cell.

"amalgamated" by rubbing its surface with mercury after it has been cleaned by dipping into dilute sulphuric acid.

Other constant cells are Grove's, where the positive plate is platinum and is plunged into strong nitric acid, separated from the sulphuric acid containing the zinc plate by a porous partition; Bunsen's, which is similar to Grove's, but with a positive plate of carbon; Leclanché's (Fig. 4), in which the acid is replaced by chloride of ammonium and the place of the positive plate is taken by carbon, which is surrounded by manganese dioxide; and Grenet's, where carbon again forms the positive plate, but with a single fluid (bichromate of potassium dissolved in dilute sulphuric acid), in which both plates are immersed. The so-called "dry" cells are modified Leclanchés. The negative plate in every one of these cells is zinc.¹

Electrodes.—The wires used in physiological experiments must always be insulated with gutta-percha or rubber, or with silk or cotton; in the latter case the insulation is rendered more effectual by dipping the covered wire into molten paraffin. For experimental purposes it is usual to place the ends of the wires (which must be clean and free from the insulating material) in some sort of holder, so that they can be more readily applied to the tissue which is to be investigated; these ends are usually



FIG. 5.—Pin-electrode.

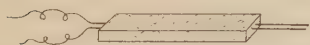


FIG. 6.—Simple cork electrode-holder.

termed the *electrodes*.² They are often made of platinum set in a vulcanite holder; but a pair of pins with fine wires soldered to their heads, constitutes a readily improvised and efficient pair of electrodes for most class purposes.

Such pin-electrodes can be passed through a small cork, or joined in parallel fashion with Chatterton's cement, with their cleaned points projecting for a few millimetres. Such an arrangement enables them to be conveniently handled.

To determine which of the two electrodes in any case is the anode and which the kathode, they may be placed in contact with a piece of blotting-paper moistened with starch solution containing iodide of potassium (*pole-testing paper*). Iodine is set free at the anode and turns the starch blue. Or filter paper which has been impregnated

¹ The accumulator or storage cell, with plates of lead and lead covered by lead peroxide, is also often used in physiological work.

² The term *electrode* means literally the "path" of the electric current, and in this sense the wires throughout are electrodes. But it has come to mean technically the ends of the wires which are used to apply the electric current to a given object (such as an animal tissue).

with phenolphthalein may be used; a red coloration appears under the kathode, sodium being set free there. Feeble differences of electrical potential are determined and estimated by other methods (galvanometer, electrometer), which will be studied later.

Non-polarisable electrodes.—Like the plates of the cell itself, metallic electrodes are capable of becoming polarised when they are in contact with the moist tissues and a current is passed continuously between them in one direction. For some experiments it is necessary to obviate this polarisation of electrodes by employing electrodes which are not polarisable. These are usually made by taking two small pieces of glass tubing open at both ends, either straight (Fig. 7) or curved (Fig. 8), and having plugged one end of such tube with china clay



FIG. 7.—Non-polarisable electrode.

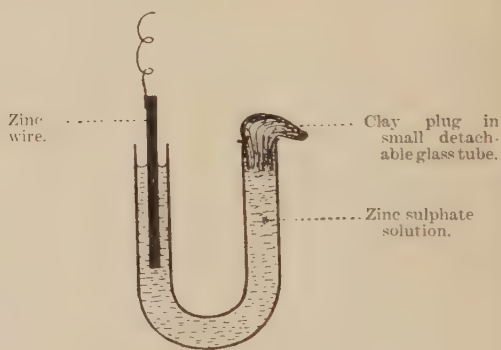


FIG. 8.—Sanderson's pattern of non-polarisable electrode.

made into a paste with salt solution, the tube is filled with saturated solution of zinc sulphate; an amalgamated zinc rod (to which one of the wires of the circuit is soldered or otherwise attached) being plunged into the zinc sulphate.

The rod is amalgamated by dipping it for a few seconds into a solution of mercury in nitric acid, washing under a tap, and polishing with cotton-wool.

A convenient form of non-polarisable electrode is that of Porter, who uses a boot-shaped tube of unglazed porcelain which is soaked with normal saline and filled with saturated solution of zinc sulphate; the amalgamated zinc rod is passed into the leg of the boot.

Keys.—Any apparatus which is used for interrupting or diverting the course of a current is called a *key* or *switch*. The keys used in physiological experiments are arranged to close and open a circuit (make and break the current); two wires forming part of the circuit



FIG. 9.—Diagram of mercury key.

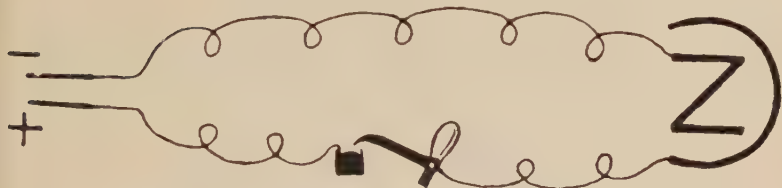


FIG. 10.—Mercury key in a battery circuit.

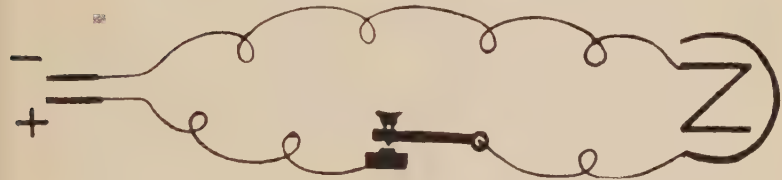


FIG. 11.—Contact key in a battery circuit

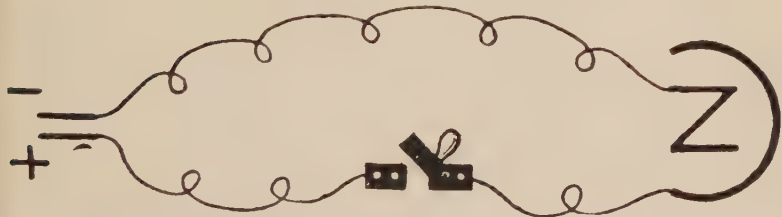


FIG. 12.—Friction key in a battery circuit ; direct method of use.

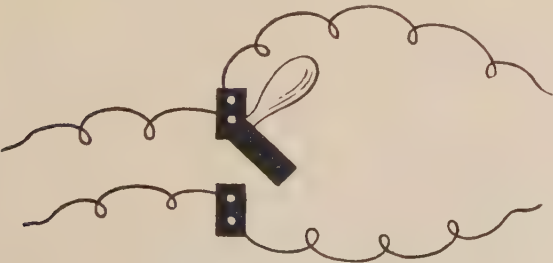


FIG. 13.—Diagram of short-circuiting key of du Bois-Reymond.

being connected together either through a pool of mercury (*mercury key*—Figs. 9 and 10); or by contact between a platinum plate and

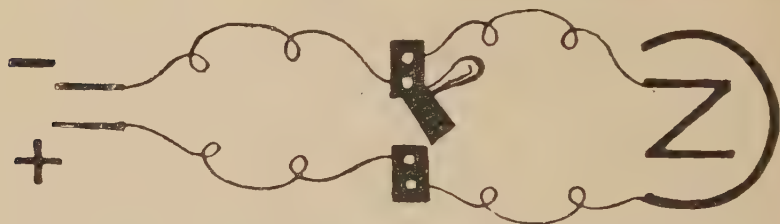


FIG. 14.—Friction key ; short-circuit method of use.

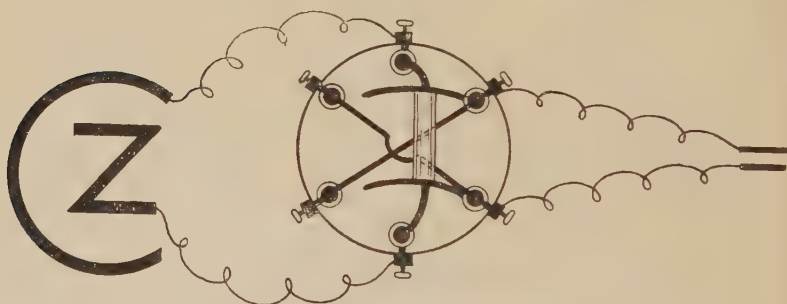


FIG. 15.—Diagram of Pohl's commutator.

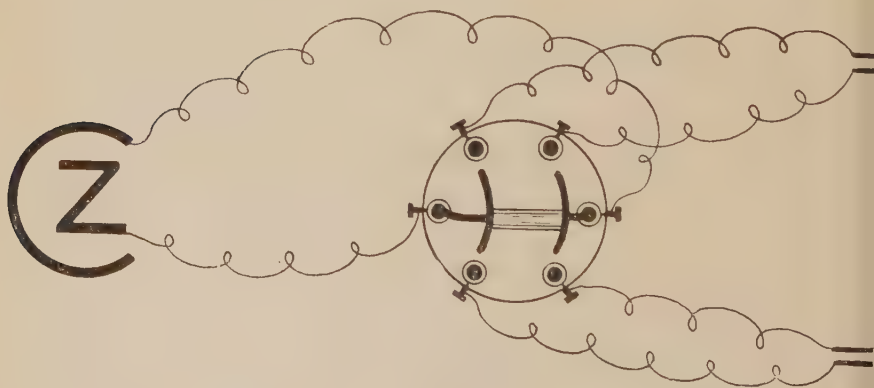


FIG. 16.—Pohl's commutator used as switch (cross wires removed).

platinum point (*contact key*—Fig. 11), as in the Morse key; or by friction contact between two brass surfaces (*friction key*), as in that known as du Bois-Reymond's (Figs. 12, 13, 14), and in the ordinary

electric-light switches. Keys are used in two ways, viz.: either to simply close or open the circuit (*direct method*—Figs. 10, 11, 12); or by bridging across a part of the circuit to offer a passage with very little resistance through the key, so that most of the current is diverted from the main circuit and from the electrodes (*short-circuit method*—Figs. 13, 14). For this purpose du Bois-Reymond's key is especially well suited.

A key which is constructed so as to cause a current to flow either in one direction or in the reverse direction in part of a circuit is called



FIG. 17.—Rotatory commutator.

a *reverser* or *commutator*. One of the most frequently used is Pohl's commutator (Fig. 15), which consists of a plate of vulcanite or other non-conducting material in which are six cups filled with mercury connected with terminals. Four of the cups are joined diagonally, two and two, by crossed wires. A rocking double bridge of copper serves, on being moved to one side or the other, to effect the reversal.

If the crossed wires are removed the Pohl can be used as a switch for diverting a current into one or other of two circuits (Fig. 16).

Other commutators have friction-contacts in place of mercury: of these the simplest are Waller's (Fig. 17), which has a rotating action;

and Malcolm's (Fig. 18), which has a sliding action. The principle is the same as the mercury commutator, and it is often convenient to dispense with mercury.

Rheochords.—A *rheochord* is an apparatus for dividing a constant

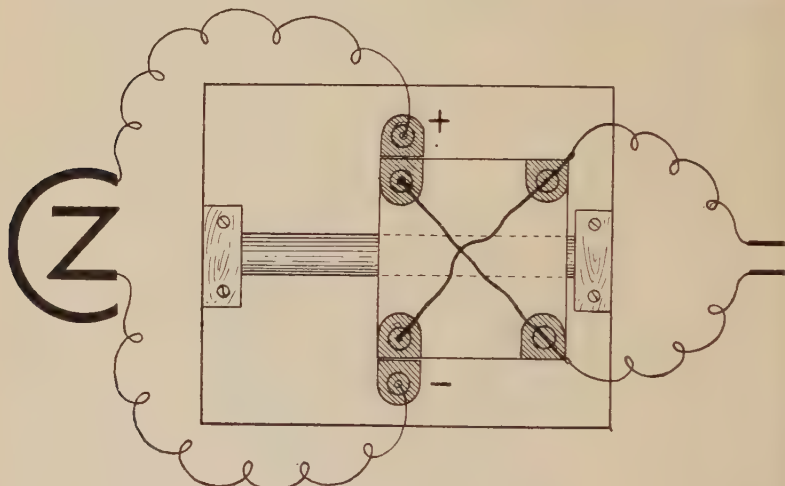


FIG. 18.—Diagram of sliding commutator.

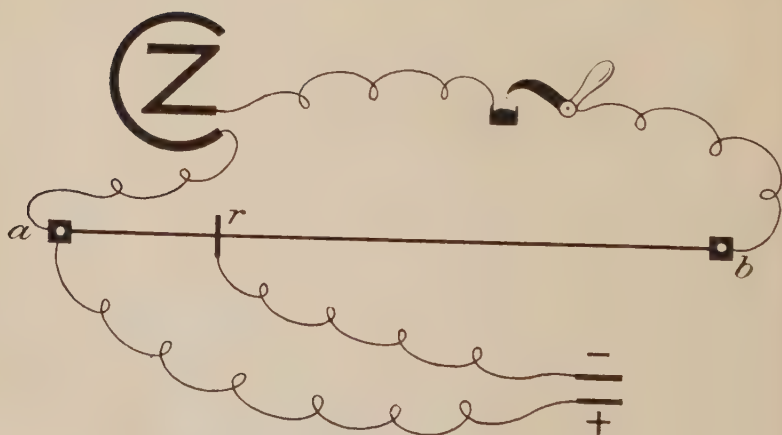


FIG. 19.—Diagram of rheochord.

current by offering a circuit of relatively small resistance which is capable of being varied so that a variable part only of the current shall pass through the experimental circuit. It usually consists of a german-silver or platinum-iridium wire of a certain known resistance

(e.g., 20 ohms), to the ends (Fig. 19, *a* and *b*) of which the wires from a cell are connected; a certain difference of potential is thereby produced at the ends of the wires. With one of these ends (*a*) another wire is connected; this forms part of the experimental circuit through which a portion of the cell current is to be conducted; this circuit

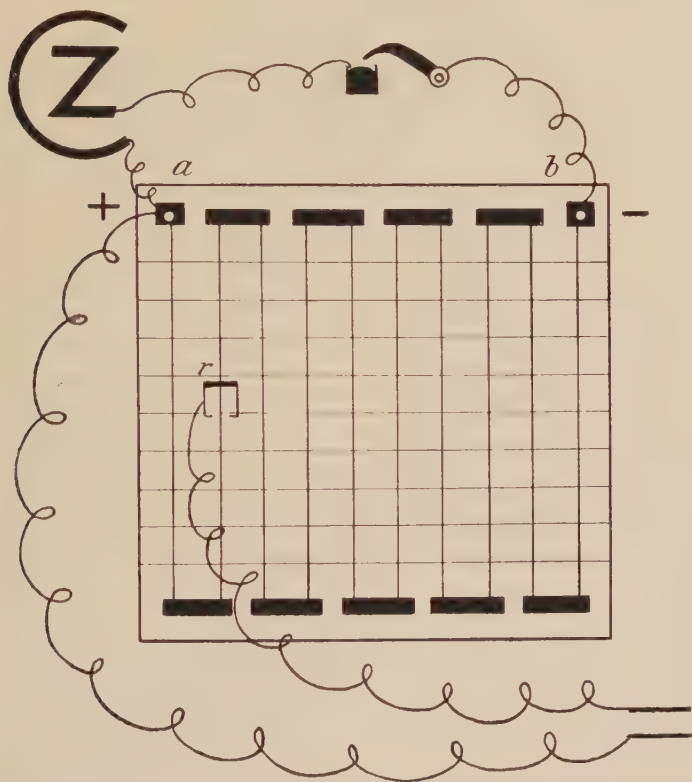


FIG. 20. —Diagram of the Oxford form of rheochord. *a*, *b*, rheochord wire zigzagged upon a mahogany board, marked by cross lines into hundredths; *r*, rider.

is completed through a wire attached to a rider (*r*) which slides along the rheochord wire.

When *r* is in contact with *b* the whole difference of potential between *a* and *b*—which depends upon the E.M.F. of the cell or battery and the resistance of the rheochord wire relative to that of the experimental circuit—is operative in producing a current through the preparation. When *r* is at the middle of the rheochord wire only

one-half of this difference of potential comes into play, and so in proportion to the distance between a and r as compared with the whole length of the wire. Thus if the wire is 100 centimetres long and r is placed at one centimetre from a , only $\frac{1}{100}$ of the total difference of potential will be operative and a proportional current will be diverted into the experimental circuit. If r is in contact with a no current is led through the preparation.

When this kind of rheochord is used, the resistance of the experimental circuit must always be relatively very great: as is invariably the case in physiological experiments, where an animal tissue forms part of the circuit.

The wire of a rheochord may be stretched straight as in Fig. 19, or, to economise space, it may be zigzagged upon a board (Fig. 20), or

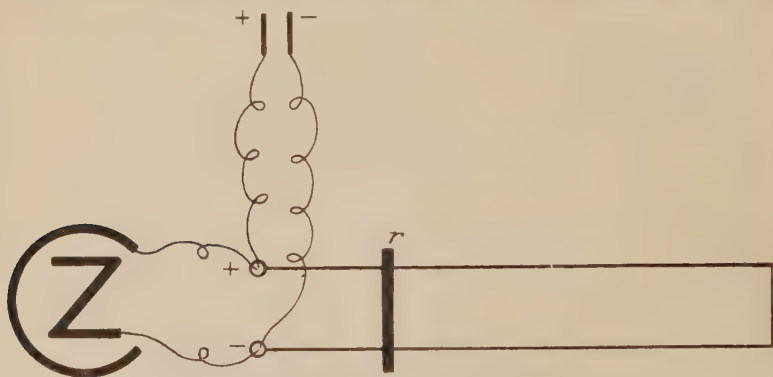


FIG. 21.—Double-wire rheochord.

arranged spirally round a vulcanite cylinder, or circularly round a disc as in du Bois-Reymond's form of instrument.

In the shunt form of rheochord there are two parallel wires, and a broad metal rider (r) bridges across and forms a short circuit between the two (Fig. 21). The cell circuit and the experimental circuit are both connected with the one end of each wire. When the rider is brought up to these ends the cell current is completely short-circuited, but when the rider is moved away from them a gradually increasing resistance is inserted into the short circuit formed by the rheochord and its rider, and proportionally more of the current passes into the experimental circuit.

Induction coil.—If the wires of two separate circuits are at any point near to and parallel with one another and if, in the first or *primary* circuit, the current of a cell is either made or broken by the closing or opening of a key, an induced current is set up in the other

or *secondary* circuit at the instant of such closing or opening, but not during the passage of the primary current. Any sudden alteration in strength in the current of the primary coil is also effective in producing an induced current in the secondary coil, the strength of the induced current being a factor of the rate of change in the primary.

In order to multiply the induction effect the two circuits always take the form of closely coiled wires (Fig. 22) (that of the secondary circuit being very fine and having very numerous coils), and to still further increase the effect the primary coil is wrapped round a core formed of a bundle of soft iron wires which are magnetised and de-

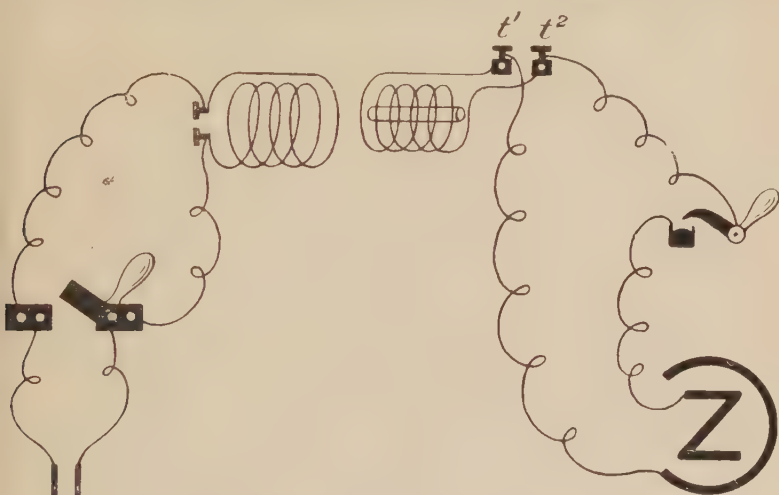


FIG. 22.—Induction coil arranged for single shocks.

magnetised on the closing and opening of the primary circuit, thereby enhancing the induction effects. The induced or secondary current thus produced is of very short duration, but has a high electromotive force.

For physiological purposes the induction coil was arranged by du Bois-Reymond so that the secondary circuit can be made to slide nearer to or farther from the primary circuit; since with the same strength of battery the nearer or farther the coils are from one another the greater or less is the strength of the induced current. The variation is not, however, proportional to the distance, but approximately inversely as the square of the distance. For producing single make and break induced shocks the primary circuit is closed and opened with a simple mercury key (Fig. 22). For multiple induced shocks most coils are fitted with an apparatus for automatically breaking and making the

primary circuit (Neef's hammer). This will be understood from the diagram shown in Fig. 23. The current is conveyed from the terminal t^3 to a steel spring sp , having a bar of soft iron at its free end, and the current passes from the spring, which has a plate of platinum upon it, to the platinum point of a screw s^1 , and thence through the primary coil. Before passing back to the cell it is conducted through

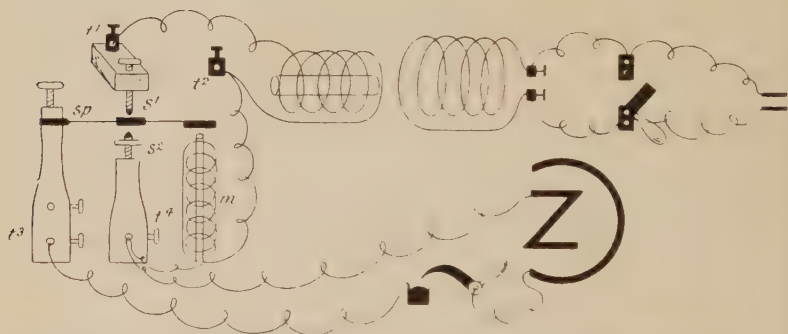


FIG. 23.—Diagram of du Bois-Reymond coil arranged for faradisation.
(For description see text.)

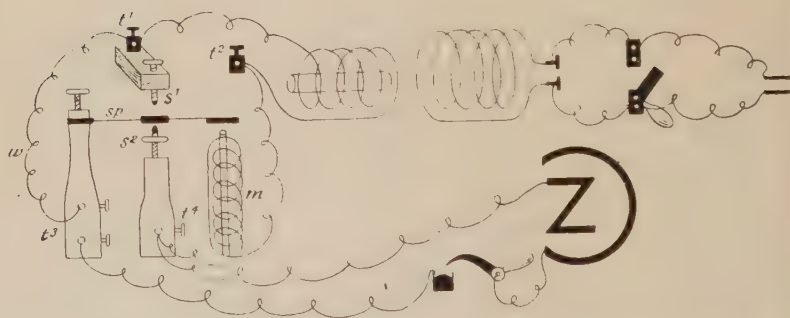


FIG. 24.—Diagram of the arrangements employed in the Helmholtz modification of du Bois-Reymond's induction coil. (For description see text.)

a small electro magnet m ; the electro-magnet being thus set in action, draws down the iron bar and with it the spring, which leaves the screw and breaks contact so that a *break* induced current is set up in the secondary coil. But, the current being broken, the electro-magnet m is no longer active, the bar springs up again, and contact is re-established between the spring and screw; this produces a *make* induced current in the secondary coil. Thus the spring vibrates to and fro, and break and make induced currents are set up in the

secondary coil many times a second, according to the rate of vibration of the spring.

These make and break shocks are unequal owing to the extra currents which are self-induced within the primary coil. The make extra-current of closure being in the opposite direction to the battery-current, diminishes the make induced-current in the secondary circuit. The break extra-current runs momentarily in the same direction as the battery-current, and would oppose its fall, but the battery-current no longer exists. The break of the battery-current therefore produces its full effect, so that the break induction shock is stronger than the make. The inequality is reduced by a modification introduced by Helmholtz. In this arrangement (Fig. 24) a wire w connects the terminals t^1 , t^3 ; the screw s^1 is raised altogether away from the spring, and does not come into use; the screw s^2 is brought nearly up to the spring. The current passes by the wire w from the terminal t^3 , directly to t^1 , thence through the primary coil and through the electro-magnet m , which draws down the iron bar and brings the spring in contact with the screw s^2 . A large part of the current now goes directly back to the cell through this contact, and is diverted from the primary coil and electro-magnet. This greatly weakens the current through the primary coil, and the equivalent of a *break* induced shock is obtained in the secondary circuit. But the electro-magnet is also weakened, so that the bar and spring fly up. This breaks the short-circuiting contact which was established between the spring and s^2 , and the whole current again passes through the primary coil, producing the equivalent of a *make* induced shock in the secondary circuit, and so on automatically. It will be observed that the primary circuit is never actually broken; but only weakened by short-circuiting. This permits both the break extra-current and the make extra-current to be effective, and tends to equalize the make and break stimuli.

The Helmholtz arrangement should always be employed for tetanic stimulation, unless the nature of the experiment contraindicates it.

Kronecker's inductorium. — Most du Bois-Reymond coils are furnished with a scale marked in millimetres to indicate the distance of the secondary from the primary coil. But the Kronecker coil is so graduated as to indicate the relative strength of the induced current (when a standard battery of constant strength is employed in the primary circuit) and the scale is marked in units as well as millimetres. Moreover, the contacts are between a platinum wire and mercury, the latter being kept clean by passing water or dilute alcohol over its surface. This gives much more constant make and break effects than the contacts between platinum point and platinum plate which are supplied with ordinary coils.

CHAPTER III

Simple Experiments Illustrating the Use of Electrical Apparatus in Physiology

1. CONNECT up a cell with a pair of wires, introducing a simple key into the circuit (Fig. 10). Place the free ends of the wires on the tongue, and close and open the key.

2. Repeat this experiment, but use a short-circuiting key (Fig. 14). Note that the effect of the current upon the tongue is now only felt when the key is open.

3. Connect a cell with electrodes through a commutator, as shown in Figs. 15, 17, and 18. Determine with pole-testing paper which is the anode and which the kathode in the two positions of the bridge of the commutator. Verify this by following out the course of the wires.

4. Connect a cell with the upper terminals t^1 , t^2 of the primary coil of the inductorium, introducing a simple key into the circuit. Connect a pair of electrodes through a short-circuiting key with the terminals of the secondary coil, and slide this coil to some distance from the primary (Fig. 22). Place the electrodes on the tongue. Alternately close and open the key in the primary circuit. Notice that induction shocks are obtained on making and breaking the primary circuit, but not during the passage of the current. Determine the distance of the secondary coil from the primary at which a make-shock and a break-shock can just be felt on the tongue. Notice that the break-shocks are much sharper than the make.

This is partly due to the extra currents taking effect at make and not at break (see p. 17), and partly to the fact that with the keys generally used the opening of the primary circuit is more sudden than its closure.

5. To show the existence of the "extra" currents, remove the secondary coil altogether and connect up the primary coil with a galvanic cell and keys in the way shown in Fig. 25. Place the electrodes on the tongue. Make and break the cell circuit by closing and opening the key k^1 . If this is done when the primary coil is included in the circuit (*i.e.*, with k^2 open as in the diagram)

the stimulus is sharp owing to the "extra" currents, but if the coil is shunted out by closing k^2 the stimulus is hardly perceptible to the tongue.

6. Instead of placing the simple key in the primary circuit (as in

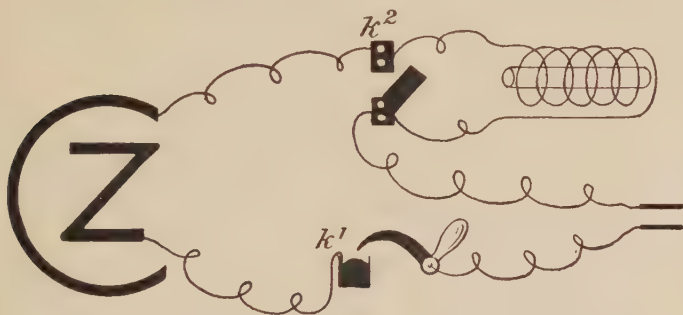


FIG. 25.—Experiment for showing effect of extra current.

Fig. 22) place it in a side circuit (Fig. 26). On closing and opening the key, shocks are still produced in the secondary circuit, although the current through the primary coil is not made and broken, but only altered in strength. The make and break shocks in the secondary coil are now more uniform, but are both weaker. This is the same effect as is obtained for rapidly interrupted shocks by the use of the Helmholtz wire (see p. 17).

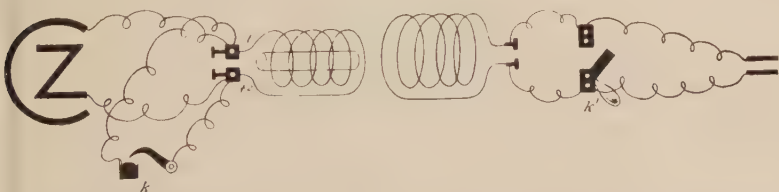


FIG. 26.—Diagram of experiment to show the effect of closing and opening a side circuit to primary coil. k , key in side circuit; k^1 , key in secondary circuit.

7. Take the secondary coil out and place it across the direction of the primary coil instead of in its usual position. The making and breaking of the primary circuit now produce no effect on the secondary circuit, but induced currents begin to show themselves if the secondary coil is placed obliquely to the primary, and are strongest when the two coils are again co-axial. This principle is embodied in Bowditch's induction coil.

8. Connect up the cell with the terminals t^3 , t^4 of the induction coil (as in Fig. 23), introducing a simple key into the circuit. Set the Neef's hammer in vibration. The electrodes from the secondary coil are to be applied to the tongue, and the distance of the secondary from the primary coil found at which the induced shocks can just be felt. Determine that these are the break shocks by raising and lowering the hammer by the hand, thereby making and breaking the primary circuit (the mercury key being closed).

9. Detach one of the wires of the electrodes from the secondary coil so that only one electrode is connected with that coil. Slide the coil home. Pass a strong current through the primary coil and set Neef's hammer going as in the last experiment. It will be found that shocks are faintly felt by the tongue, although only the one electrode is in connexion with the secondary coil and the secondary circuit is broken (*unipolar induction*).¹ It is on account of this possibility of stimulating through only one pole that a simple key is never used in the secondary circuit, but always a short-circuiting key, which is introduced in the manner shown in Fig. 22. No shocks can pass to the electrodes when the key is closed, since the coil is then short-circuited; only when the key is open are the shocks conducted to the electrodes. On the other hand, in the primary or cell circuit a simple key is always used; were a short-circuiting key placed here the cell would rapidly run down.

10. Connect up a cell with the induction coil, using Helmholtz's modification (Fig. 24). As in experiment 8, find the distance of the secondary from the primary coil at which the induced shocks can just be felt on the tongue, and determine that the make and break shocks are now nearly equal by raising and lowering the spring by the hand. Both are markedly diminished as compared with the ordinary arrangement.

¹ The explanation of this is that the body acts as a condenser which becomes charged and discharged through the electrode applied to the tongue.

CHAPTER IV

The Muscle-Nerve Preparation

THE central nervous system of a frog is destroyed by cutting through the spinal cord at the occipito-atlantoid ligament and passing a blanket pin into the skull and down the cord. Notice that the muscles of the

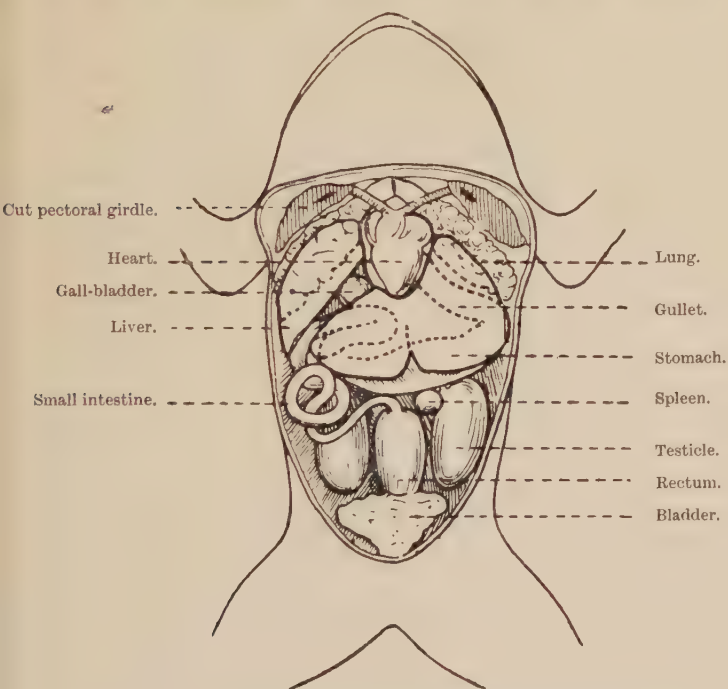


FIG. 27.—Viscera of frog. The liver is shown in outline, and the parts concealed by it are indicated by dotted lines.

trunk and limbs are thrown into contraction when the cord is being destroyed. Make a circular incision round the trunk just below the upper limbs through the skin only, and, seizing the skin covering the lower part, strip it off from both hind limbs. Lay the frog on its back

on a flat cork or glass plate, and open the abdomen and thorax freely but carefully. Notice the viscera (Fig. 27)—heart and lungs, liver, stomach, intestines, ovaries and oviducts or testes, bladder. Cut through the lower end of the intestine and through its attached mesentery. On raising it, two elongated red bodies—the kidneys—are seen at the back of the abdomen, partly covering the nerves which are passing down to the hind limbs. Remove the kidneys without touching the nerves. Now hold the frog up by its legs so that the

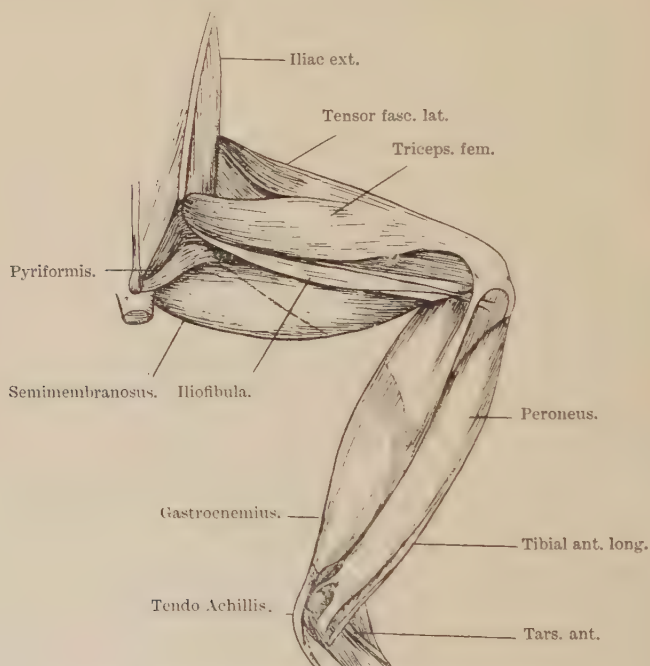


FIG. 28.—Muscles of frog-leg; dorsal aspect (Gaupp).

viscera hang towards the head, and sever the lower end of the vertebral column with strong scissors so as to separate the fore part of the trunk and the viscera from the pelvis and hind limbs. Lay the latter preparation on a clean glass plate or on a piece of paraffined paper on the frog-cork. Note the several muscles which are seen on the front and back of the lower limbs (Figs. 28, 29).

The thin, flat sartorius is seen crossing obliquely over the front of the thigh. It is readily isolated by cutting the tibial attachment away with a piece of the bone, raising this, and snipping through the fascia on either side of the muscle, thus separating it right up to its

iliac attachment. Notice the twitch which occurs when the nerve, which enters the under surface about its middle, is cut through. The upper end of the muscle may be left attached to the ilium, or its bony attachment may be cut away with it and the muscle thus completely isolated. Its uppermost part contains no nerve fibres, and can be used to show that, independently of nerve, muscle responds to all forms of stimulation (electrical, mechanical, thermal, and osmotic).

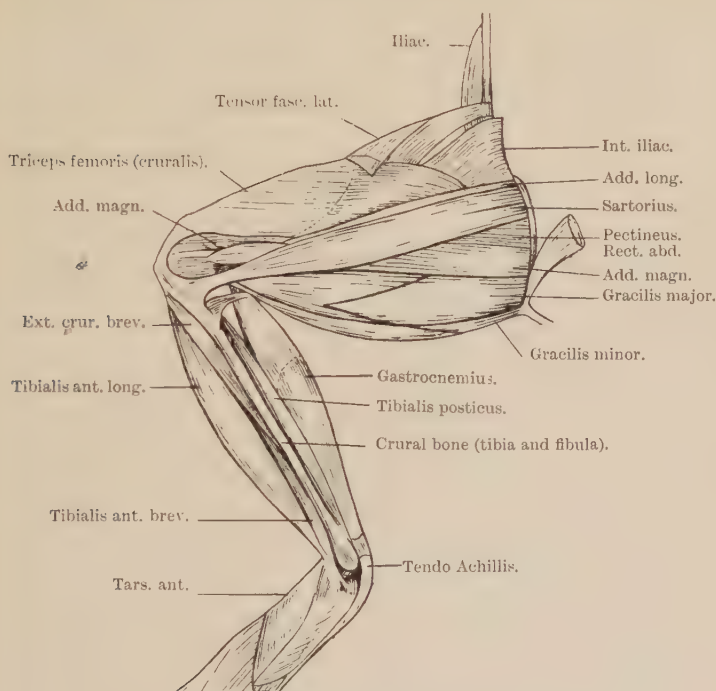


FIG. 29.—Muscles of frog-leg ; ventral aspect (Gaupp).

The gastrocnemius is generally used for experiments. Tie a thread round its tendon (tendo Achillis), and cut this away from the calcaneum. Holding it by the thread, tear the muscle upwards away from the tibia, and sever this bone just below the knee.

Next bring to view the sciatic nerve. Separate the muscles at the back of the thigh by the aid of two pairs of forceps, keeping to the medial of the two chief intermuscular septa, and the nerve will be seen, accompanied by the femoral vessels. On no account touch the nerve, but separate the muscles from it so as to expose it freely.

If only a short piece of nerve is required, a wet thread may be tied

round the uppermost end of the length of nerve displayed, and the nerve may be cut across above the thread. Then, holding it up gently by the thread and passing a pair of straight scissors below and parallel to the nerve, its branches to the thigh muscles are successively severed, and the nerve is separated as far as the back of the knee-joint. Notice that as each branch is snipped the muscle which it supplies contracts (mechanical stimulation). Lay the nerve thus isolated upon the gastrocnemius muscle. Then cut through the middle of the femur, and clear the attachments of the thigh muscles away from the lower end of that bone. You now have a preparation consisting of the knee-joint with portions of the femur and tibia, the gastrocnemius muscle, and the sciatic nerve; this is termed a *muscle-nerve preparation*.

For some experiments a longer nerve is needed. To obtain this the sciatic nerve is to be exposed as before from behind, but not tied or cut; it should indeed not be touched in its course by any instrument. Then seize the urostyle with forceps, and cut it and the muscles attached to it entirely away with scissors. The nerves previously seen behind the kidneys are now exposed from the back; they are continuous on each side with the corresponding sciatic nerve. To isolate the nerve along its whole length, sever the attachment of the ilium to the sacrum. Split the end of the spinal column longitudinally with scissors, and, holding one-half with forceps, lift it up obliquely, but not at too sharp an angle, along with the nerves issuing from it to form the sciatic. Gradually dissect out the nerve from above down as before described, snipping the lateral branches with scissors (without touching the main nerve) until the back of the knee is reached. Lay the long piece of nerve thus isolated upon the gastrocnemius muscle, and, as before, cut through the middle of the femur, clearing the attachments of the thigh-muscles away from its lower end; you now have a *nerve-muscle preparation with long nerve*. Place a piece of paper impregnated with paraffin on the frog-cork, and lay the nerve out clear of the muscle, fixing a pair of electrodes so that the nerve lies across them. Keep both muscle and nerve—but especially the latter—wet with normal salt solution or Ringer's solution.

With either of these nerve-muscle preparations the following experiments, which are, for the most part, similar to those already performed upon the tongue, are to be made. Note down all your results.

Excitation by galvanic current.—Determine that making or breaking the circuit of a cell or battery is a stimulus to the nerve, whereas the passage of the current usually¹ produces no obvious

¹ For exceptions see Chapter XI.

effect. It is proper to use non-polarisable electrodes whenever a galvanic current is led through a preparation.

A simple form of galvanic element is furnished by two wires, one of copper, the other of iron or zinc. If these are placed with one end of each in contact with the moist nerve-muscle preparation, and if the other ends are made to touch one another, the muscle will contract; as in Galvani's original experiment.

Fleischl's rheonome is designed to show that not only the change of potential but that the suddenness of the change is an important factor in stimulating with a galvanic current. The rheonome consists of a bridge composed of two curved pieces of zinc capable of being rotated about a raised centre. One end of each piece has a terminal attached

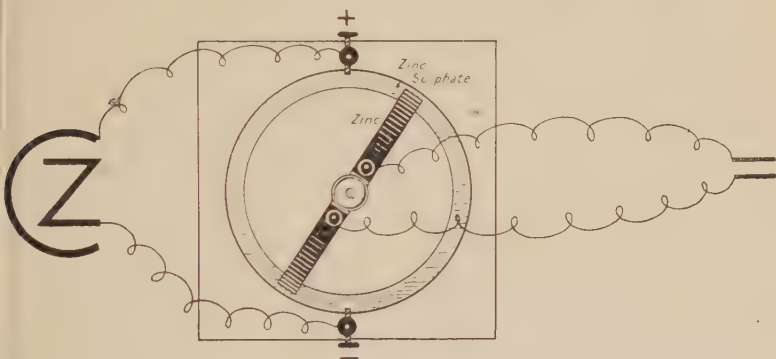


FIG. 30. —Diagram of Fleischl's rheonome.

to it (upper terminals); the other end—which should be amalgamated—dips into saturated solution of zinc sulphate contained in a circular groove in the wooden base of the instrument. Wires from a battery are brought to opposite sides of the groove and come into connexion with the zinc sulphate solution by amalgamated zinc terminals (lower terminals). The upper terminals are brought into relation with a muscle-nerve preparation by other wires, and when the battery circuit is closed part of its current passes to the preparation, while part is short-circuited through the zinc sulphate. The amount of short-circuiting depends upon the position of the rotating bridge. Most current passes through the preparation when the ends of the bridge are opposite the lower or battery terminals. On now rotating the bridge this current is diminished, and it vanishes when the rotation has attained 90° of the circle, gradually increasing again as this point is passed. If the rotation is slow, there is no stimulation of the preparation, in spite

of the variation in amount of current ; but if quick, the muscle-nerve responds to each movement of the bridge.

The rheonome may also be made with a copper bridge, the ends of which dip into solution of sulphate of copper.

Excitation by induced current ; Determination of excitability of a nerve.—An induction shock is a stimulus, and the break induction shock a far stronger stimulus than the make. Get the minimal effect of each by sliding the secondary coil to the necessary distance from the primary, and make a note as to the respective positions of the secondary coil. This gives a measure of the excitability of the nerve. Its excitability to tetanisation (use the Neef's hammer with and without the Helmholtz wire) is determined in the same way.

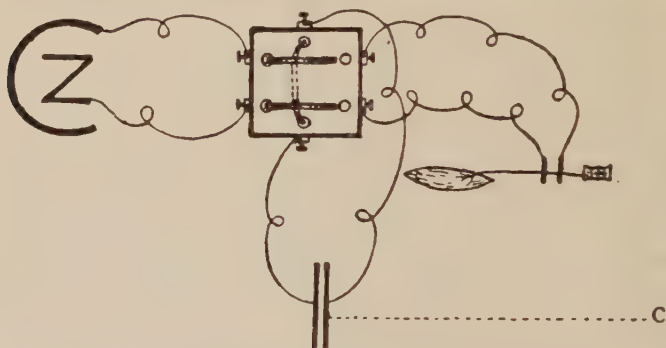


FIG. 31.—Stimulation of nerve by condenser discharge.

Reaction of nerve and muscle to galvanic and faradic excitation.—If the above experiment is tried (*a*) with a nerve-muscle preparation and (*b*) with nerveless muscle (the nerves within the muscle are paralysed by curari), it will be found that the nerve will react to a weaker stimulus than the muscle when induction shocks are employed ; but if the make and break of a galvanic circuit be used as the stimulus the muscle will respond to the weaker stimulus. Plain muscle shows this even more strikingly.

Chronaxy.—A galvanic current must, in order to produce excitation, not only be of sufficient strength, but must also be allowed to act for a sufficient time on the preparation which is to be stimulated. The minimum duration of the action of such a stimulating current is termed the *chronaxy* (time value) of the tissue. Different kinds of nerve and muscle vary greatly in their chronaxy: that of ordinary skeletal muscle and myelinated nerve being, for example, much shorter than that of involuntary muscle and non-myelinated nerve.

The following description will give a general idea of the manner in which the chronaxy of an excitable tissue, such as the nerve passing to a muscle, is measured:—

Connect a constant battery with a rheochord (p. 12) to which a pair of non-polarizable electrodes is attached, so that the amount of current passing to the preparation can be varied. Under ordinary circumstances, *e.g.*, if the battery circuit is closed and opened with a mercury key operated by hand, the preparation will be excited at the closing and again at the opening of the circuit. If the closing and opening were to follow one another at too short an interval, *i.e.*, if the current is conducted through the nerve only for a very small fraction of a second, no excitation would be produced by it. But such very short duration of the passage of the current cannot be produced by the hand, and some special apparatus, which enables the circuit to be made and broken with an extremely small interval between, must be employed. An apparatus which serves this purpose is the Keith-Lucas pendulum¹: this can be regulated to close and open the circuit so as to allow the current to pass through the nerve for periods of time which are extremely short, and can be varied by suitable adjustments.

Use the battery and rheochord, and allow the current to pass without the Keith-Lucas pendulum. Starting with a current which produces no effect, the strength is increased until the nerve just becomes excited by it, *i.e.*, its muscle just gives a perceptible twitch on closing the circuit. The E.M.F. of the current which produces this is measured: it is termed the *rheobase*. The E.M.F. of the stimulating current is now raised until it is exactly double the rheobase: this is employed for measuring the chronaxy of the tissue. For this purpose it is not allowed to pass through the excitable tissue for an indefinite time, but only for a very short period, which may at first be too short (say, $\frac{1}{10000}$ sec.) for the current to produce any stimulating effect. The period during which the current is allowed to pass is now gradually increased by moving the adjustments on the Keith-Lucas pendulum until a point is reached at which a response just becomes visible. The duration of this *effective* period can be exactly measured by the pendulum, and represents the chronaxy of the particular nerve or other tissue which is being investigated.

Another method of measuring chronaxy is to employ condensers of varying capacity. For, assuming that the resistance in the circuit remains unaltered, the duration of the current on discharge is directly proportional to the capacity of the condenser. A condenser of 3 microfarads capacity is charged to different potentials until it just excites the tissue on discharge.¹ This furnishes the

¹ The discharge of such a condenser will occupy about $\frac{1}{100}$ sec. under the conditions of the experiment.

rheobase. The E.M.F. for charging is now, as before, doubled, and this is employed to charge a series of condensers, the capacity of which varies from 0.001 to 0.5 microfarad, in steps of 0.001 microfarad. Beginning with the lowest, one of these is found which just serves to stimulate the preparation, a resistance of 10,000 ohms and a shunt being introduced into the stimulating circuit. The chronaxy in seconds of the tissue is found from the following formula:—

$$0.37 \times R \times C$$

where R is the resistance in ohms and C the capacity in farads of the condenser.

Gotch's experiment.—Cooling a nerve causes it to react to galvanic and faradic stimulation in the same way as muscle. The upper end of the nerve of a nerve-muscle preparation is cooled by laying it on a tube through which ice-cold water is passing (the muscle itself must not be allowed to come anywhere near the cooled tube). If, now, the cooled part of the nerve is stimulated, it will be found to be less sensitive to faradic and more sensitive to galvanic stimulation than a part nearer the muscle which has not been cooled. Cooling the nerve also diminishes the rate of conduction of nerve impulses along the cooled portion (see p. 53), and increases the chronaxy.

Unipolar induction.—It is possible to stimulate the nerve when it is connected by only one wire with the secondary coil; hence the necessity for using a short-circuit key to prevent *unipolar induction* (see p. 20). It is best for this experiment to place the secondary coil close to the primary and to make use of the automatic interrupter.

Excitation by condenser discharge.—The discharge of a condenser through a nerve acts as a stimulus. Arrange the apparatus as shown in Fig. 31, in which c is a condenser made by covering a sheet of glass with tinfoil on both sides. The sheets of tinfoil are connected with a battery of two or three cells for a few seconds, and then, by turning the switch, are connected with the nerve, the battery being cut off by the same movement.

Mechanical excitation.—A nerve (or muscle) can be stimulated by mechanical means—*e.g.*, by tapping it gently or by allowing mercury to drop upon it (Fig. 32). The effect of a mechanical stimulus is also seen whenever a nerve is cut or pinched, but a severe injury abolishes its conducting functions.

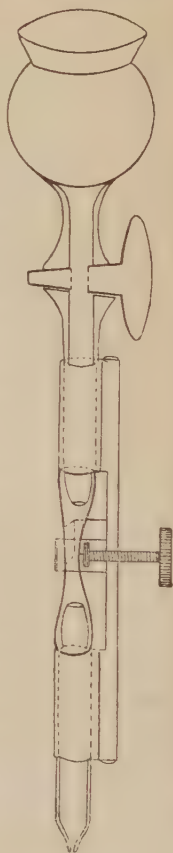


FIG. 32.—Diagram of mercury dropper to produce mechanical stimulation of a nerve. Natural size.

Thermal excitation.—A nerve (or muscle) is stimulated if touched with a hot wire; or with a wire cooled to below 0°C .

Osmotic excitation.—A nerve can be stimulated by withdrawal of water, caused by placing brine or glycerine upon it. The salt and the glycerine both act by abstracting water.

Excitation by drying.—The withdrawal of water by drying also acts as a stimulus to nerve. When the nerve begins to dry, its muscle twitches.¹

Addition of water may also act as a stimulus, especially with muscle. If distilled water is injected into the blood-vessels of an animal, all the muscles are thrown into contraction: this is, however, followed by paralysis. The effect is in part due to the abstraction of calcium salts from the muscle.

¹ This twitching is a frequent source of puzzle to the beginner; it is always a sign that he has not been careful to keep the nerve moist.

CHAPTER V

The Recording of Muscular Contractions

MUSCULAR contractions are recorded upon a metal drum covered with highly glazed paper, and caused to revolve by clockwork, or some other form of motor, at a regular rate. With a drum of six inches diameter one revolution in a second is a conveniently fast speed. The glazed paper is blackened by holding a gas flame containing benzine vapour against it while the drum is revolving. The paper must fit evenly and tightly, or it will become burnt.

The contraction of the muscle is amplified by a lever (myograph lever), which may be straight (Fig. 33), but which may also conveniently take the crank form (Fig. 34). In this case the fulcrum of the lever is near one end of a cork plate, to which the muscle is fastened by a pin passed through the knee-joint: the tendon is attached to the short arm of the lever by means of a thread. The cork plate must be covered with paraffined paper. The lever should be weighted with a 20- or 30-gramme weight, attached to it close to the fulcrum, and should be so adjusted as to be nearly horizontal, but with the end a little lower than the fulcrum. The muscle is kept stretched by the weight, so that the connecting thread is taut. Under these circumstances the muscle is said to be *free-weighted*.

There should always be a screw near the fulcrum which is intended to support the lever in certain experiments. The screw can be adjusted so that the muscle and thread are not freely stretched, and only become so after the muscle has begun to contract; the muscle is then described as *after-loaded*.

In the Keith-Lucas crank myograph the muscle-nerve preparation is enclosed in a vulcanite trough; the muscle is kept immersed in Ringer's fluid; the bony attachment of the muscle is fixed by a pin, and electrodes are introduced through holes in the vulcanite. The whole is covered by a glass plate to prevent evaporation.

The following points must be attended to in every graphic record in which a lever is employed:—(1) On no account must the lever point be directed obliquely upwards: the result of doing this is to distort the curves which are recorded; (2) the lever must be directed

by hand after each record. Stimulate (*a*) by closing (*b*) by opening the mercury key, beginning with the secondary coil at such a distance

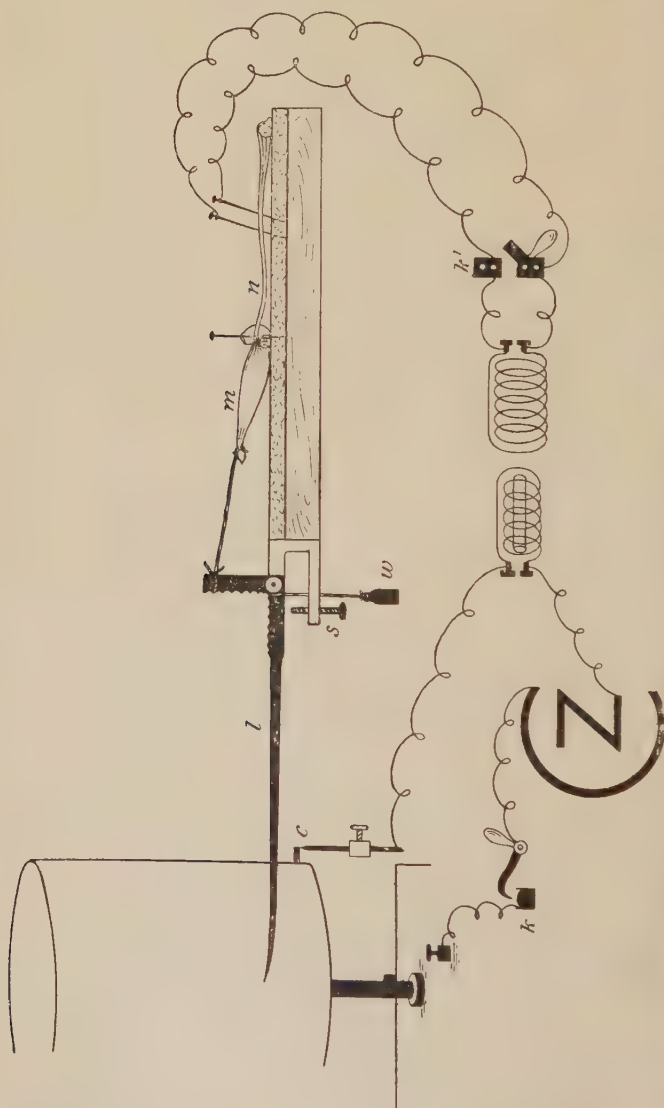


FIG. 34.—Arrangement of apparatus for obtaining an isotonic muscle curve. *c*, drum contact in primary circuit; *k*, mercury key in drum circuit; *k'*, du Bois-Reymond key in secondary circuit; from this key wires pass to the pin-electrodes on which the nerve, *n*, is placed; *m*, muscle; *l*, crank-lever; *w*, weight; *s*, after-loading screw (not in use).

from the primary that no effect is obtained, and gradually diminishing the distance until the effects are maximal. The ordinates obtained represent the extent of contraction of the muscle (as magnified by the

lever) with different strengths of stimulus. Beyond a certain point no further contraction is obtained. The contractions are then said to be maximal. The submaximal contractions are due to the fact that with the weaker induction currents only some of the fibres are stimulated by the current, so that the whole of the muscle is not thrown into contraction.

The tracings show the relation of the extent of contraction to the strength of the stimulus.

The simple muscle-curve.—Arrange the muscle and myograph lever as in the last experiment, but with the drum in the primary circuit of the induction coil (in the manner shown in Fig. 34), so that, as the drum revolves, a pin (*c*) which projects from it, by just touching a needle fixed outside, instantaneously makes and breaks the circuit at each revolution. With a rapidly revolving drum the two induction shocks thereby produced act as a single stimulus, since the second falls within the refractory period which follows the first. With a slower ~~rate~~ of drum the make-shock must be cut out by moving the secondary coil to a distance at which it becomes ineffective.¹ Before the lever is allowed actually to touch the cylinder, determine that all the apparatus is in working order, and at what distance of the secondary from the primary the induction shock is effective in causing a maximal contraction when the drum is made to revolve. Do not allow the muscle to become fatigued by many excitations before recording its contraction.

Now bring the lever point so as lightly to touch the blackened paper, *using the stop of the myograph stand to prevent the point pressing too hard against the paper*. When the stop is used in this way the lever point can be removed at any time from the paper and brought back again so as to press with exactly the same force as before; *it is absolutely essential to make use of the stop in all recording experiments in which comparisons of different curves upon the same surface have to be made*; failure to do so will invalidate all results.

Start the drum revolving, but keep the short-circuit key (*k'*) closed so that no stimulus reaches the nerve; the lever point will describe a horizontal line (abscissa). Whilst the drum is still revolving open the short-circuit key, but close it again the instant the muscle has contracted; immediately afterwards remove the lever point from the drum, before this has had time to perform another revolution. A simple muscle curve will thus be described.

To mark the point of stimulation, move the drum slowly round by

¹ It is also possible to employ a single induction shock as the stimulus, by introducing a break key into the primary circuit and making the pin open this key as the drum revolves.

hand until the projecting pin just strikes the needle where contact is made (as in the diagram, Fig. 34); bring the lever point against the smoked surface as far as the stop will allow, and raise the lever about half an inch by the finger. The distance between this mark, which indicates the moment when the stimulus was put into the nerve, and the rise of the curve, which indicates the commencement of the contraction of the muscle, gives the *period of latent stimulation*. To measure this period, as well as the duration of the contraction and

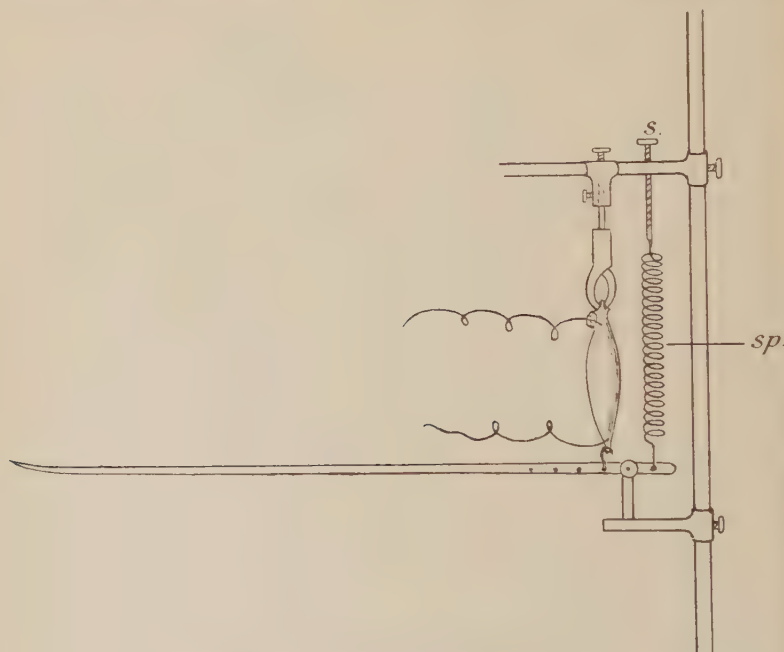


FIG. 35.—Method of studying isometric contraction. *sp*, spiral spring; *s*, screw for regulating its tension.

relaxation of the muscle, remove the lever point from the smoked surface, set the drum revolving at the same rate as before, and allow a tuning-fork of known rate, *e.g.*, one hundred vibrations per second, to record a time tracing, either directly or by an electro-magnet; putting the writing point attached to the tuning-fork or electro-magnet against the drum during a single revolution only. Cut through the paper without scoring the surface of the drum. Lay it on the table, and write upon it name, date and description. Then pass it through the varnishing trough, and hang it up to dry. When dry, cut out the part of the tracing which is required and paste it into your note-book.

Effect of heating and cooling the muscle upon its contraction.—

The same nerve-muscle preparation may be used, the apparatus being arranged exactly as in the last experiment. Mark on a new abscissa the point of stimulation. Then take the following curves on this abscissa:—

1. A simple muscle curve at the room temperature.
2. A simple curve after warming the muscle by dropping Ringer's solution, warmed to about 25°C ., upon the muscle.
3. A simple curve after cooling the muscle, placing a small piece of ice in contact with it for two or three minutes.

Finally, take a time tracing below the abscissa.

Notice the effect of heat and cold respectively upon the period of latency and upon the amount and duration of the contraction.

Isometric contraction.—If the contracting muscle is prevented from shortening, or allowed only to shorten to so small an extent that it remains practically of the same length throughout, the contraction is said to be isometric. It is recorded by attaching the muscle very close to the fulcrum of the muscle lever, which is held down by a strong spiral spring (Fig. 35) instead of by a weight. All the other arrangements of the experiment are the same as with the method already employed, where the muscle is free to shorten and raise a weight so that its tension remains constant throughout (isotonic contraction).

Action of veratrine on muscular contraction.—**The hyoglossus preparation.**—In a large frog, killed by pithing, cut away the whole of the lower jaw, along with the tongue and hyoid bone. Tie a thread to the tongue near its tip and another near its fixed extremity, and cut this away from the hyoid. The tongue thus separated includes the hyoglossus muscles, which run through it from the hyoid bone, and the preparation can be used in the same way as the gastrocnemius muscle, the hyoid end being fixed by a pin to the myograph cork and the tip connected by its thread with the myograph lever. A smaller weight must be used than in the case of the gastrocnemius, since the hyoglossus muscles are far weaker. Probably the weight of the lever alone will be sufficient. Insert pin-electrodes near the fixed end so that induction shocks will stimulate all the fibres of both hyoglossus muscles.

Arrange the apparatus to take a muscle curve in the usual way. If the speed of the drum is the same as before (one revolution per second), the curve is more prolonged than that of the gastrocnemius, for the contraction of the hyoglossus is slower than that of the gastrocnemius. It is better, therefore, especially in investigating the

action of veratrine, to use a much slower rate—one revolution in about 10 seconds—since this drug enormously delays the relaxation of muscle.

A normal muscle curve is first described, the point of stimulation being marked in the usual way. Then with a hypodermic syringe a drop or two of veratrine acetate solution (1 in 300) is injected under the mucous membrane of the tongue, so that the drug is brought into contact with the fibres of the hyoglossi. After three minutes take another muscle curve. Describe a time tracing below the abscissa. If the preparation is excited repeatedly, it will be found that the contractions lose their prolonged character, which, however, returns after a period of rest.

The same method can be used for investigating the action of other drugs upon muscular contraction.

If such muscles as the sartorius or gastrocnemius are to be investigated as to the action of drugs upon them they are immersed in Ringer's solution; either in a Keith-Lucas muscle-bath (see p. 30) or in the manner shown in Fig. 56. The drug is added to the Ringer and allowed to soak into the muscle.

CHAPTER VI

The Nerveless Muscle

Action of curari.—The brain of a frog is destroyed by passing a sharp splinter of wood through the occipital foramen after cutting through the skin and occipito-atlantoid ligament. The blood-vessels of one leg are ligatured, care being taken to avoid injuring the accompanying sciatic nerve. A drop or two of 1 per cent. solution of curari is now injected under the skin of the back. After a short time the drug will have penetrated to all parts of the body except the ligatured leg.¹ The following observations and experiments may then be made:—

1. Notice that the whole body is paralysed except the ligatured limb.

2. On tapping any of the paralysed parts the foot on the ligatured side is moved—therefore not only are its muscles and nerve endings not paralysed but the conducting power of its nerves, afferent as well as efferent, and the reflex functions of the spinal cord, are not abolished.

3. Strip the skin off both legs and isolate both sets of sciatic nerves at the back of the abdomen. Tie their upper ends and cut them away from the vertebral column. Excite both sets of nerves high up, placing them upon the same electrodes, and observe the difference of effect. Excitation of the nerve of the limb which has been exposed to the poison produces no contraction of its muscles; excitation of the nerve of the ligatured limb produces the usual effect. Now stimulate the muscles of the two limbs, applying the electrodes directly to them. The muscles of the poisoned limb react like those of the normal limb, but the liminal stimulation² must be greater. Determine at what distance of the secondary coil from the primary a response is obtained in each case.

The conclusion is that neither the nerve fibres, sensory and motor,

¹ This method, which was devised by Claude Bernard, is applicable in general to the study of the action of drugs on the nervous and muscular systems.

² The stimulation which is only just effective, i.e., the least stimulation which is responded to.

nor the nerve-centres, nor the muscle-fibres are paralysed, but that the poison has produced paralysis by severing the connexion between motor nerve-fibres and muscle-fibres, probably at the end-plates.

The paralyzing action of curari can also be shown by keeping a muscle-nerve preparation in Ringer's solution in which a little curari has been dissolved. It will be found that after a time the muscle will cease to respond to stimulation of its nerve, although it will contract readily if the muscle itself is stimulated. As a control, another preparation may be taken, and its nerve alone placed in the same solution during the same period, the muscle being supported above the level of the fluid. The preparation will respond to every stimulation of its nerve.

It is best to use a sartorius muscle-nerve preparation for this experiment on account of the length of time necessary for the curari to penetrate the gastrocnemius.

For the mode of preparing the sartorius—the nerve of which must be kept in continuity with the main trunk—see p. 22.

Muscle-wave.—Separate from the remaining thigh muscles the adductor muscles (gracilis and semimembranosus: see Figs. 28, 29) of a frog which has been poisoned with curari to eliminate the intramuscular nerves. Leave the attachments to the tibia. Cut this bone through just below these attachments, and also sever the tibia from the femur at the knee joint. It is then easy to complete the separation of the muscles up to their iliac attachments; a small fragment of the ilium may be cut away and removed along with them. Tie a thread to the tibial and another to the iliac attachment, stretch the muscular mass lightly between these threads, and fasten to the cork by a couple of pins at one end and a pair of pin-electrodes at the other end of the muscle. Allow two long light levers (which can be made of straws, working in simple brass holders capable of being pinned to the cork) to rest upon the muscle near each end close to their fulcra, and let the points of the levers write lightly on the drum, one exactly above the other (Fig. 36). When the muscle contracts, its swelling raises first the lever near to the electrodes, and later the one at the further end. The movements of the levers are recorded upon the drum, and curves are obtained of the swelling of the muscle during its contraction in the same manner as the curves of shortening of the gastrocnemius were obtained in previous experiments. The drum must move at a fast rate, and the levers should be directed obliquely downwards: much more so than in the ordinary method.

Connect the pair of pin electrodes with a du Bois-Reymond key (*k*) in the secondary circuit. Describe an abscissa, and mark the

point of stimulation as in previous experiments by raising the end of each lever by the hand when the projecting pin on the drum just touches the vertical needle (see p. 33), *making use of the stop*. Then take the two tracings of the contraction of the muscle, letting the drum revolve once only, and removing the levers the instant the curves are completed. The difference of latency of the two curves represents the time which it has taken for the wave of contraction

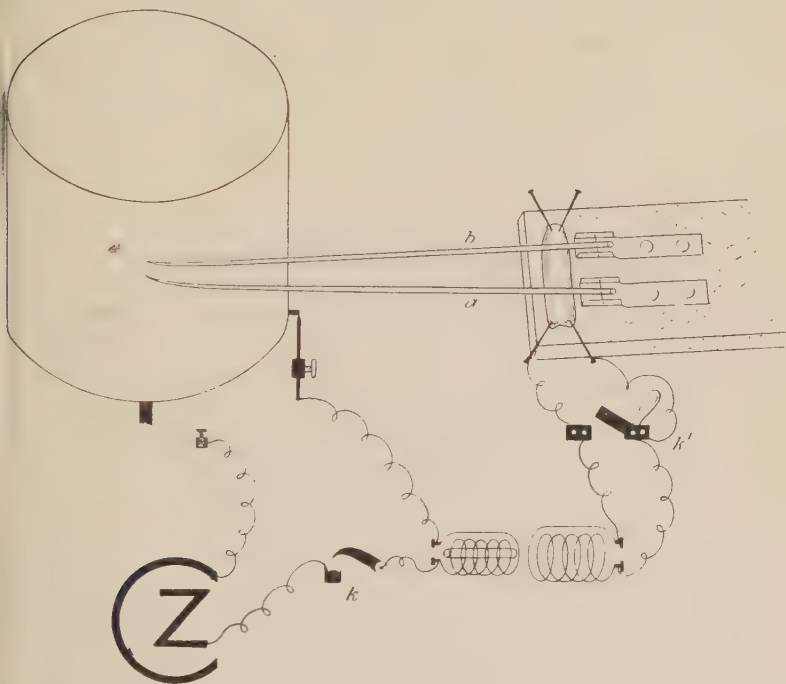


FIG. 36.—Diagram of Aaby's experiment for recording the muscle wave. *a, b*, light straw levers resting on the muscle, which is curarised; *k, k'*, keys in primary and secondary circuits.

to pass along the length of the fibres intervening between the two places on which the levers rest. Take a time tracing, and measure this difference, and from it and the length of muscle traversed by the wave (measure with compasses) calculate the rate of propagation of the muscle wave.

It is essential for the success of this experiment that the muscles used should have most of the fibres running longitudinally and parallel with one another. If very large frogs are obtainable the two sartorius

muscles may be used with advantage instead of the adductor preparation described.

Another method of obtaining the curve of swelling of a contracting muscle, better adapted, however, for mammalian muscle than for the frog, is to use the *pince myographique* or *myographic forceps* of Marey (Fig. 37). The muscle is grasped by this, and its contraction affects

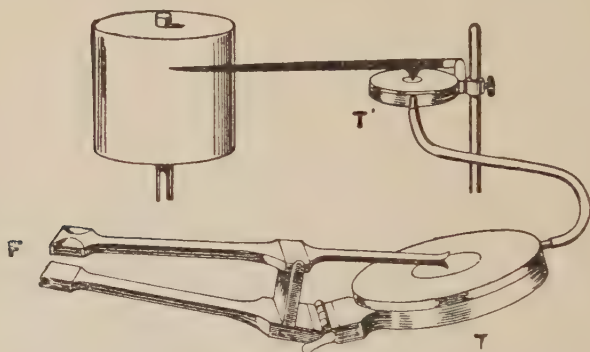


FIG. 37.—Myographic forceps of Marey. F, forceps for grasping the muscle, the contraction of which is to be recorded. The two blades of the forceps are drawn together by an india-rubber band. T, receiving tambour, the air in which is compressed by the swelling of the muscle, and from which the pressure is transmitted by an india-rubber tube to T', the recording tambour, the lever of which writes on a revolving drum.

a tambour (T) which is connected by rubber tubing to another tambour (T'), writing upon the drum. The muscle is stimulated (1) at the point of application of the forceps, and (2) at some distance from the forceps. The difference of time between the two resulting curves is measured, and the rate of passage of the muscle wave calculated therefrom

CHAPTER VII

Effect of Successive Stimuli upon a Muscle-Nerve Preparation

Superposition. — Arrange the muscle-nerve preparation on the myograph and connect the drum in the primary circuit in the manner employed to record a simple muscle curve (Fig. 34). Place the secondary coil at such a distance from the primary that the excitation produced by a single pin projecting from its circumference and striking the needle in its revolution produces a maximal effect; describe a normal muscle curve in the usual way. Then insert a second pin at varying intervals so that the excitation which it produces will affect the nerve at different intervals after the first excitation; viz., (*a*) during the rise of the first curve, (*b*) near the top of the first curve, (*c*) during the decline of the first curve. Take these double tracings at different levels of the paper, each one on its own abscissa.

Effect of several successive stimuli; tetanus. — For studying the effect on a nerve-muscle preparation of a rapid succession of stimuli a vibrating steel reed is used to make or break the primary circuit of the induction coil by allowing a wire attached to its end to dip into and out of a cup of mercury, the surface of which should be clean and covered with dilute alcohol. The rate of vibration of the reed depends upon its length, which can be varied by clamping it at different places; it is marked at points for producing vibrations of ten, fifteen, twenty, and thirty per second (Fig. 38). The secondary coil should be placed at such a distance from the primary that only the break shock is effective. The drum should revolve at moderate speed (one revolution in 20 to 30 seconds).

Attach the muscle to the lever of the myograph in the usual way; place the nerve upon the electrodes; set the reed vibrating; set the drum revolving and bring the lever point against it, *using the stop*; open the key in the secondary circuit for about a second; take the lever point away from the drum. A tracing is to be taken in this way at each of the above rates, each tracing on its own abscissa; add a time marking.

Record of voluntary contraction. — A voluntary muscular contrac-

tion of the finger muscles may be recorded by resting the hand across the myograph plate and tying a thread to the abducted forefinger, the other end of the thread being attached to the short arm of the lever; this is to be heavily weighted or to be held down by a strong elastic band. On adducting the finger the lever is raised, and a curve is described on the moving drum which bears a close resemblance to an incomplete and somewhat irregular tetanus produced by ten or twelve stimulations per second.

It must not be concluded that this represents the rate of the successive individual contractions which fuse to form the voluntary

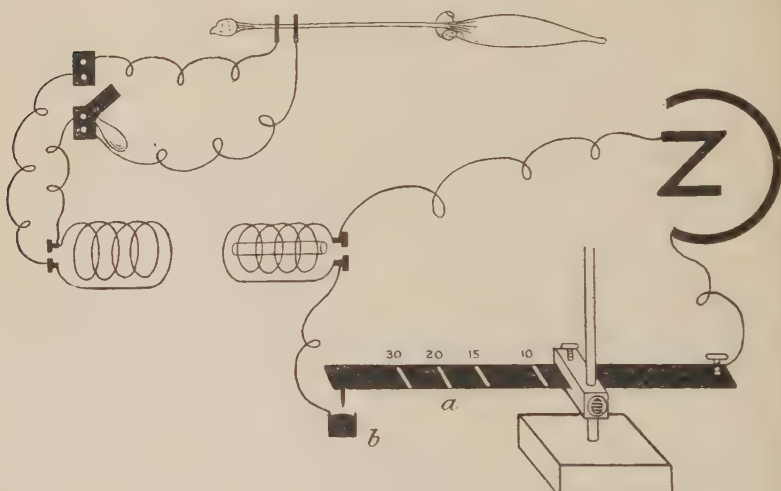


FIG. 38. — Experiment to investigate the genesis of tetanus. *a*, flat steel spring marked at intervals with the number of vibrations corresponding to certain lengths of the spring; *b*, mercury cup into and out of which a pin attached to the spring dips.

contractions, for it has been shown by photographic records of the capillary electrometer (see p. 65) that in a voluntary contraction there are not less than fifty electrical changes per second, and this probably also represents the number of mechanical changes which succeed one another in a voluntary contraction. The mode of causation of the irregular waves is not understood.

Another method of obtaining the curve of a voluntary contraction is by the use of a *transmission myograph*, which consists of two tambours connected by india-rubber tubing. The first or receiving tambour (which may be represented by an ordinary Marey's cardio-

graph; see Fig. 66) is fixed against the masseter muscle; when this muscle is made to contract voluntarily, its movements are communicated to the air within the cardiograph, and the differences of pressure produced are transmitted to the second or recording tambour, which writes upon a revolving drum.

Sound of a voluntary contracting muscle.—Place the tips of the middle fingers in the ears, and contract the muscles of the arm strongly. A rumbling sound is heard, which is caused by the vibration of the contracting fibres. The sound actually heard is modified by the resonance of the drum of the ear, and cannot be taken to indicate the rate of rhythm of contraction.

CHAPTER VIII

Work of Muscle ; Extensibility of Muscle

THE experiments to be performed on these subjects are recorded upon a stationary drum, which is moved onwards for about 5 millimetres by hand after each record.

Make a muscle preparation, preferably the sartorius (see p. 22), place it on a myograph, and arrange that it shall be stimulated, either directly or through its nerve, by induction shocks. Arrange a mercury key in the primary circuit (which is not to include the drum) and a short-circuit key in the secondary circuit. It is best in these experiments to use tetanic stimuli furnished by the Neef's hammer ; and preferable to employ the Helmholtz modification (Fig. 24). The lever should have a light scale pan suspended from it ; such a scale pan can be made from the lid of a pill-box. The scale pan is made to hang upon the long arm of the lever at the same distance from the fulcrum as the attachment of the thread which connects the muscle to the short arm. Determine:—

1. The effect upon the lift, the weight being constant (say about 30 grammes), of a gradual increase in the strength of the stimulus from minimal to maximal.

Note down on the curve the distances of the secondary coil at which the results recorded are obtained.

2. The amount of work which the muscle performs in lifting different weights, the stimulus being constant and maximal and the muscle free-weighted. Beginning with the weight of the scale pan alone, weights are gradually added, and the muscle being stimulated, an ordinate is described for each additional weight.

Note down the weight which corresponds with each ordinate and the height of the ordinate. The exact height to which the weight is raised is obtained by dividing the height of each ordinate by the magnifying extent of the lever. The work done is calculated as $\text{weight} \times \text{height}$. The load with which the greatest amount of work is done by the muscle is termed the *optimal load*. Determine from your calculations the optimal load for the muscle you are using.

Another result is yielded in this experiment: viz., the effect of the

gradually increasing weights in producing extension of muscle in the resting and contracted conditions respectively. For it is obvious that the lowermost point of any ordinate described by the muscle represents the length to which the resting muscle is extended by the particular weight, and the top of the ordinate the length to which the muscle

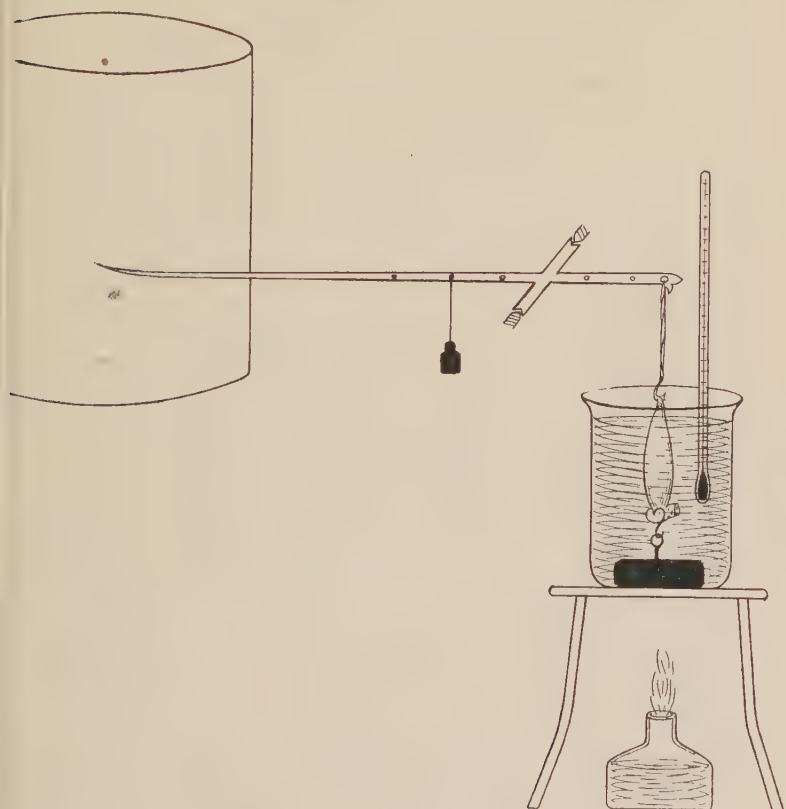


FIG. 39.—Experiment for investigating the effect of heat on the extensibility of muscle.

when contracted is extended by the same weight. If the ordinates are at regular distances apart, a line joining their lowermost ends gives the curve of extension of the resting muscle, and a line joining the tops of the ordinates the curves of extension of the contracting muscle. Further, if the weights are removed in succession and ordinates are again described after each such removal, curves of

recovery from extension—*i.e.*, of retraction—can be obtained. This experiment can be conveniently performed separately, the result obtained giving the curves of extensibility and retractility of resting muscle which may be compared with similar results obtained by substituting a rubber band for the muscle.

3. The effect of after-loading (p. 30). Take a series of contraction ordinates, using a maximal stimulus and a constant weight (say about 30 grammes). Begin with the muscle free-weighted, and by using the screw stop beneath the lever(s, Fig. 34) raise the latter so that the muscle and connecting thread are somewhat slackened. Under these circumstances the muscle will not begin to raise the weight until its contraction has proceeded to a certain extent; this shows the effect of after-loading. Describe two series of contraction ordinates (*a*) with a gradual increase of after-load, and (*b*) with the muscle only just so much after-loaded as to prevent it from being stretched by the successive weights employed. Calculate the amount of work done under both these conditions, and compare with that performed by the free-weighted muscle.

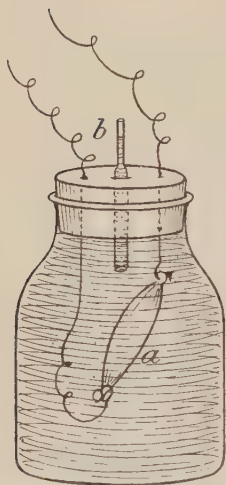


FIG. 40.—Experiment to determine if a muscle alters in volume during contraction. *a*, muscle in Ringer's solution; *b*, capillary.

Effect of heat on the extensibility of muscle.—Take a sartorius or gastrocnemius muscle and fix one end to a heavy disc of metal provided with a hook: place the disc and muscle in a beaker of Ringer's solution (Fig. 39). Attach the other end of the muscle by means of a thread to the short arm of a lightly weighted lever of the first order, so that when the muscle shortens the long arm of the lever is raised. Let the point of the lever write on a *very slowly* moving drum. Arrange a small gas or spirit flame to heat the beaker of Ringer's solution, which should be provided with a thermometer. Notice the effect of the gradual rise of temperature upon the length of the muscle as recorded by the lever. Note especially that at certain temperatures—which correspond with the coagulation temperatures of the muscle-proteins—there is a marked shortening. (The final contraction corresponds with the coagulation temperature of the collagenous matter, *i.e.*, of the connective tissue, and is not muscular.) After no further shortening is produced, remove the flame and allow the liquid to cool. There is no reversal of the contraction of the muscle, which remains stiff and

completely coagulated (heat rigor). If the muscle is cut and tested with blue litmus or neutral red paper it will now be found to be acid.

During contraction a muscle does not alter in volume.—Take a wide-mouthed bottle with well-fitting paraffined cork (Fig. 40). Through the cork are passed a glass tube drawn out above the cork to capillary size, two copper wires of unequal length, the longer one coiled spirally and each ending below in a sharp hook: above the cork each wire ends in a loop. Fill the bottle to the brim with boiled and subsequently cooled Ringer's solution. Attach a fresh muscle by its two ends to the hooks, lower into the bottle, and press the cork in securely: the fluid should completely fill the bottle and capillary tube to the exclusion of air-bubbles. Draw a little of the fluid out of the capillary by filter paper, and mark the level at which the fluid then stands. Hook wires from the secondary coil to the loops above mentioned, and tetanise the muscle. If there were a diminution of volume the level of the water in the capillary would fall.

CHAPTER IX

Fatigue of Muscle and Nerve

Effects of fatigue on muscle. (a) **On the form of the muscle curve.**—Take a nerve-muscle preparation and fit it up as for recording the simple muscle curve (Fig. 34). Make an abscissa, and mark, as usual, upon it the point of stimulation. Take a normal curve with the muscle free-weighted. Remove the writing point from the drum, which is then allowed to revolve continuously and to stimulate the muscle at every revolution. After fifty of such excitations without record, apply the lever point again to the drum (making use, of course, of the stop), and let the muscle describe another curve at the same place as the first. Remove the writing point again for the duration of fifty excitations, and repeat the above procedure, and so on a number of times until the fatigue curves are pronounced. Notice the effects of fatigue upon muscle, in prolonging the latency period, diminishing the amount and slowing the course of its contraction, and greatly delaying, and at length even preventing, its relaxation.

A fatigue curve or series of curves can also be obtained by allowing the lever point to remain in contact with the cylinder during the whole of the experiment, and thus recording every contraction; but the individual curves in a tracing so obtained are very numerous, and tend to obscure one another.

(b) **On the extent of contraction.**—The effect of fatigue upon the extent of contraction is best recorded upon a stationary drum, moved by hand about half a millimetre after each excitation; or on a very slowly moving drum: the extent of the contraction is shown by the ordinates described by the lever. If the slowest rate of movement of the drum (1 mm. per second or less) is used, arrange to make and break the primary circuit about every half-second. This can be done either by closing and opening a key by the hand, or by allowing a metallic bridge, actuated mechanically (*e.g.*, by a metronome), to close and open a gap between two mercury cups in the circuit. Use maximal stimuli. Keep the point of the lever—which must be free-weighted—against the smoked paper, and record every contraction. In this way a *continuous fatigue curve* is obtained, exhibiting the

effect of fatigue upon the amount of contraction, and also on the extensibility of the muscle both in rest and in contraction. Notice the "staircase" (gradual rise of the ordinates) at the beginning of the curve and the "contracture" (permanent contraction remainder) near its termination. Carry the experiment to complete exhaustion—i.e., until the stimuli produce no further perceptible effect through the nerve. Application of the electrodes to the muscle itself will now be found to cause contraction—not that the nerve itself is fatigued, but that the junction of nerve and muscle is affected by the fatigue products before the muscle substance itself.

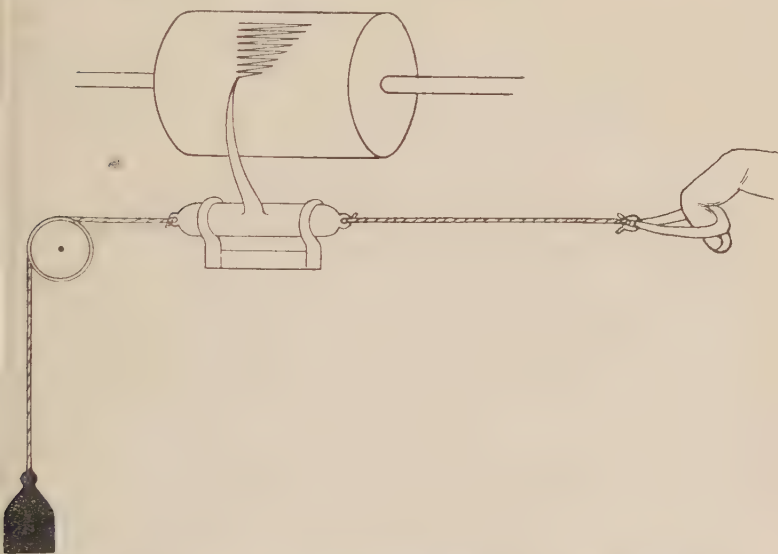


FIG. 41.—Diagram of Mosso's ergograph for the investigation of fatigue in the human subject.

Recovery.—Allow the preparation to rest, keeping it moist with Ringer's solution. After 15 or 20 minutes again test the effect of a stimulus. Notice that there is a certain amount of recovery from the fatigue, even in a preparation such as this in which no blood is circulating. In muscle in which the circulation is maintained, fatigue not only comes on more slowly but is more rapidly recovered from, since the circulating blood removes the fatigue products.

Reaction of the fatigued muscle.—Cut across a muscle which is completely fatigued, and apply blue litmus or neutral red paper to it. Notice that the paper is changed, indicating the production of acid fatigue products. Compare the reaction with that of a piece of

fresh, unfatigued muscle. Muscle which has died and passed into rigor—whether natural or the effect of heat (see p. 47)—is also acid.

Fatigue in voluntary contraction.—This is investigated by the *ergograph* (Fig. 41), the muscles of the fingers being fatigued by causing them to repeatedly raise a heavy weight or repeatedly deflect a strong spring. The extent of the contractions is recorded upon a very slowly revolving drum, and a fatigue curve or *ergogram*—which always shows individual peculiarities—is thereby produced in the same manner as with the frog muscle-nerve preparation.

This experiment can also be conveniently made—in the same way as the record of voluntary contraction described in Chapter VII.—with the adductor indicis muscle, employing the ordinary crank myograph, the lever of which is held down by a strong rubber band.

In Mosso's ergograph and Porter's modification the records are made upon a horizontal drum; in Waller's modification (dynamograph), in which a strong spring is used in place of a weight, the drum is vertical.

In the case of voluntary contractions the result is complicated by the fact that fatigue of nerve-cells in the central nervous system occurs before fatigue of the muscle itself or of the nerve-endings in the muscle. This fact can be shown by direct faradic stimulation of the median nerve (or of the long flexors of the fingers) after the fatigue curve is complete. It is found that the muscles can still be made to contract by such peripherally applied stimuli.

CHAPTER X

Conduction in Nerve

Conduction of nerve impulses may take place in both directions:
Kühne's experiment.—Remove the gracilis with part of its entering nerve; lay it on a glass plate, with its inner surface uppermost. The nerve is seen to give branches upwards and downwards; as a matter of fact each nerve fibre divides into two branches, one for the upper and the other for the lower part of the muscle, which has a tendinous intersection obliquely across its middle. The middle part of the muscle can be entirely cut through here without injuring these nerves, and the two parts of the muscle will then only be united by the forked nerves.

If the ends of the nerves in either of the pieces of the muscle are stimulated, whether electrically, osmotically (salt), or mechanically (by snipping with scissors), both pieces contract.

Rate of transmission of nerve impulse.—Make a nerve-muscle preparation in the usual way; fix it upon the myograph, and lay the nerve out upon two pairs of electrodes, one placed as near the muscle as possible, the other close to the vertebral column. With the nerve of a large frog 5 centimetres (nearly 2 inches) will intervene between the two. Place a commutator without cross wires in the secondary circuit, and arrange so that by moving the bridge of the commutator the induction shocks can be switched on to one or other pair of electrodes. The drum is included in the primary circuit, and a short-circuit key in the secondary (Fig. 42). The lever should have a slightly greater dip than under ordinary circumstances, so as to ensure a sharp rise of the writing point.

Two muscle curves are now successively taken with a fast rate of cylinder and a maximal stimulus. The stimulus is applied to the nerve, first, close to the muscle, and, second, close to the vertebral column. The muscle curves are both taken in exactly the same way, and with exactly the same precautions as to the use of the stop, etc., detailed in Chapter V., and both curves are to be traced upon the one abscissa, a time tracing being written a little above the abscissa, so as to

intersect the rise of the curves. It will be found that the curves are not quite coincident, but that one succeeds the other by a very

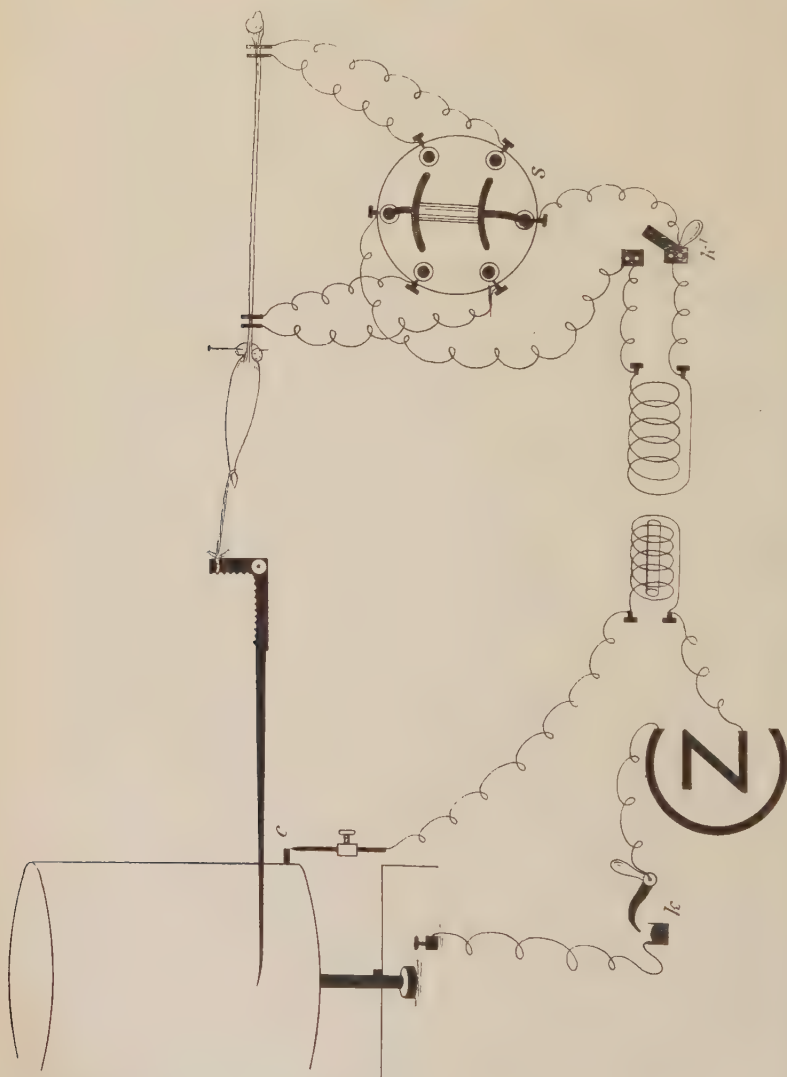


FIG. 42.—Experiment for recording the differences of latency of a nerve-muscle preparation when the nerve is stimulated (a) near the vertebral column, (b) near the muscle. *k*, mercury key in primary circuit; *c*, drum-contact in primary circuit; *K*, key in secondary circuit; *K'*, drum-contact in secondary circuit.

small interval. This interval represents the time occupied by the transmission of the nerve impulse along the length of nerve between the two pairs of electrodes.

The interval is relatively small compared with the total latency period of the muscle-nerve preparation. It can be rendered more evident if the nerve (not the muscle) is cooled (p. 28). To measure it accurately a longer nerve and faster rate of movement must be taken. This is obtained by the use of the *pendulum myograph*, upon which the contraction of the human thumb muscles is recorded. The electrodes used consist of wash-leather pads soaked with strong salt solution. One electrode, large and flat, is fixed against the skin of the upper part of the back, the other smaller one being applied respectively over the median nerve at the elbow and over the brachial plexus above the clavicle; the length of nerve between these points is about 12 inches. The muscle-contraction in this case is recorded by tambours or by the *pince myographique* (p. 40).

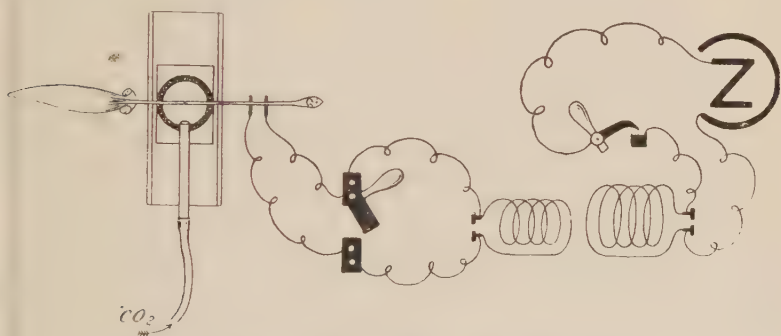


FIG. 43.—Effect of carbon dioxide on conduction in nerve.

Effect of various substances on nerve-conduction : carbonic acid ; ether vapour ; chloroform vapour.—Take a nerve-muscle preparation and lay the nerve across and partly sunk in a ring of putty or plasticine placed upon a glass slide, to which a tube is cemented so that a current of air charged with gases or vapours can be conducted over the nerve. A cover glass is placed upon the ring: the end of the nerve projects beyond this and rests upon a pair of electrodes (Fig. 43). The slide is fixed to the myograph cork by plasticine and the muscle is attached to the cork and lever in the usual way.

Find the minimal stimulus which will just produce a steady tetanus of the muscle, the drum being set to revolve slowly (one revolution in 30 seconds); then pass a current of CO_2 over the intervening nerve, and notice its effect in blocking the nerve-impulse. Remove the CO_2 by a current of air, and observe the result.

Other experiments may be made with ether vapour and chloroform

vapour instead of CO_2 . It will be found that ether acts like CO_2 , but more powerfully. Chloroform vapour is more powerful than ether; after a short exposure to it the nerve does not recover its power of conduction on readmitting air; it has, in fact, been killed.

Blocking by a galvanic current—Bernstein's experiment.—To exhibit the blocking effect of a galvanic current upon nerve, take a muscle-nerve preparation with long nerve and attach the muscle to the myograph lever in the usual manner, so that its contractions may be recorded upon a slowly moving drum (one revolution in 30 seconds).

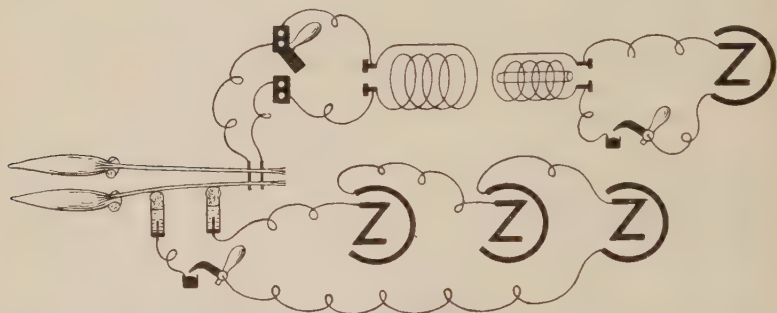


FIG. 44.—Diagram of Bernstein's experiment to illustrate the blocking effect of a constant current upon conduction of nerve impulses.

Apply stimulating electrodes from the secondary coil to the part of the nerve near the vertebral column, using the Neef's hammer (with Helmholtz wire) for tetanisation and a strength of stimulus just sufficient to produce a maximal contraction. Apply a pair of non-polarisable electrodes, connected through a mercury key with a battery of three Daniell cells, arranged so that the current can be passed up the nerve¹ (polarising circuit). Take a tracing of the muscle during tetanisation, and whilst this is progressing close the polarising circuit. The tetanus at once ceases, to be renewed on again opening that circuit, and so on repeatedly.

This experiment can be varied in the manner shown in Fig. 44; using two nerve-muscle preparations, and merely observing the contraction of the muscles, without recording it.

¹ The polarising current will act as a block to the conduction of the excitation equally well if passed downwards; but in that case it is itself liable to produce stimulation should the preparation be very excitable (see p. 59).

CHAPTER XI

Conditions of Excitation of Nerve and Muscle by the Galvanic Current

THE passage of a galvanic current through a nerve or muscle produces secondary polarisation of these tissues, caused by the accumulation of positive and negative ions at or near the poles of the constant current. This polarisation is accompanied by certain physiological changes, the tissue being more excitable in the neighbourhood of the negative pole or kathode, and less excitable in the neighbourhood of the positive pole or anode. These effects—both physical and physiological—spread for some distance beyond the actual poles. And not only is the tissue rendered more excitable by the kathode, but this itself sets up excitation, which, in the case of a muscle, may cause its contraction, not only at the moment of closure, but during the whole time of passage of the current. On breaking the circuit the part of the nerve which was more excitable during the passage of the current becomes instantaneously less so than the rest (physiological rebound). On the other hand, the presence at the anode of a constant current not only renders the tissue less excitable whilst the current is passing, but on breaking the circuit there is again a rebound; the part which was the less excitable becoming the more excitable; this passage from less to greater excitability again acts as a stimulus. Hence, when a constant current is sent through a nerve or muscle, there is excitation at the kathode on making and at the anode on breaking the circuit. But the latter furnishes a rather weaker excitation than the former.

Polar excitation of muscle.—1. Engelmann's sartorius experiment. —A curarised sartorius is connected with a pair of non-polarisable electrodes which are joined up through a mercury key with a battery (Fig. 45). It will be observed that the twitch begins at the kathode when the circuit is closed; indeed, the muscle may remain more or less contracted at that end during the whole time of the passage of a strong current. On the other hand, on opening the circuit the twitch begins near the anode, and may again be followed by a prolonged contraction. These prolonged contractions show that the excitation is

produced not only at the make and break, but also during the passage, and for a short time after the cessation of a strong constant current.

2. An instructive variation of this experiment is to dissect out the rectus abdominis muscles of a curarised frog, and place the non-polarisable electrodes one in contact with the anterior, the other with the posterior end of the flat muscular mass (Fig. 46). The muscles are divided into several segments by tendinous septa, and it will be seen that during the passage of the constant current each of these segments has the part directed towards the kathode in a condition of contraction, and the part directed towards the anode in a condition of relaxation.

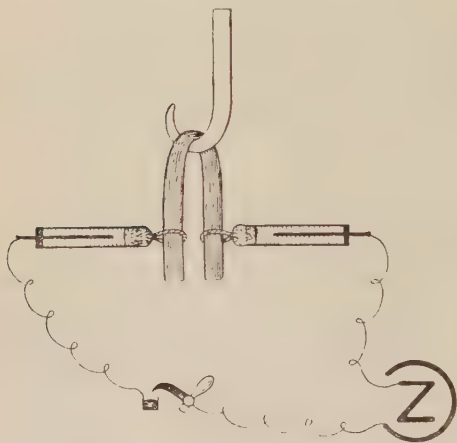


FIG. 45.—Polar effects of constant current upon curarised sartorius.

3. The effect of the poles of a constant current upon cardiac muscle can be exhibited on the frog's heart. The frog is killed by destroying the brain, and the heart is exposed *in situ*. Using non-polarisable electrodes and the whole current of a Daniell cell with a



FIG. 46.—Polar stimulation of rectus abdominis. *m*, muscle, curarised and stretched between two pieces of cork.

mercury key and a commutator in the circuit, place one electrode in the mouth or on any part of the body of the frog, and connect the other, by means of a short piece of cotton-wool wetted with Ringer's solution and drawn to a point, with the heart, so as to touch it near

the base of the ventricle. If this electrode is the anode, on closing the key it will be observed that the part of the ventricle underneath it does not participate in the contractions, but remains quiescent, and bulges during general systole: on opening the key this part passes into systole, even during general diastole (physiological rebound). If the current is reversed and the cotton-wool is made the kathode, contrary effects are obtained.

Polar excitation of nerve.—Take a muscle-nerve preparation with as long a nerve as possible and arrange it on the myograph. Non-polarisable electrodes, connected with a constant battery through a mercury key, are placed—the anode in contact with the uppermost end of the nerve, the kathode in contact with the lowermost end, *i.e.*, close to the muscle. Insert an electro-magnetic signal into the circuit and cause it to mark on the drum just below the myograph lever. Record two contractions, one produced by closing the mercury key, the other (on a different abscissa) by opening it. Make a time tracing below, and measure exactly the period of latency in each case, *i.e.*, the time elapsing between the movement of the electro-magnetic signal and the commencement of rise of the curve. Notice that it is slightly greater as the result of breaking the circuit than on making (by the time taken for the nerve impulse to traverse the length of nerve), since the excitation at *breaking* is at the anode, *i.e.*, at a point of the nerve furthest from the muscle, whereas on *making* the excitation was at the kathode, *i.e.*, close to the muscle.

If, as represented in Fig. 47, an ascending current is used instead of a descending one, the result is complicated by the blocking effect of the constant current on conduction (see p. 54). Thus, on *making* such an ascending current, if it were a strong one, the excitation being at the kathode, *i.e.*, at the uppermost end of the nerve, and the intermediate part of the nerve being at the same moment traversed by the current, this would block the passage of the nerve impulse generated at the kathode, and no contraction would result. Therefore, instead of obtaining a contraction at both make and break, only the break would produce a visible effect under these circumstances. On the other hand, if the constant current is weak, its removal may not be followed by contraction of the muscle, because the breaking of such a current furnishes a smaller excitation than its making.

The varying effects of opening and closing a galvanic current (misnamed “the law of contraction”) are illustrated by an experiment devised by Pflüger. The nerve of a nerve-muscle preparation is placed in non-polarisable electrodes, which are connected with a battery of at least three Daniell cells through a commutator and rheochord: a mercury key is introduced into the circuit (Fig. 48). Beginning with

a *very weak current*, the rider of the rheochord being brought near to the end *a* of the rheochord wire (see Figs. 19, 20), determine the effect

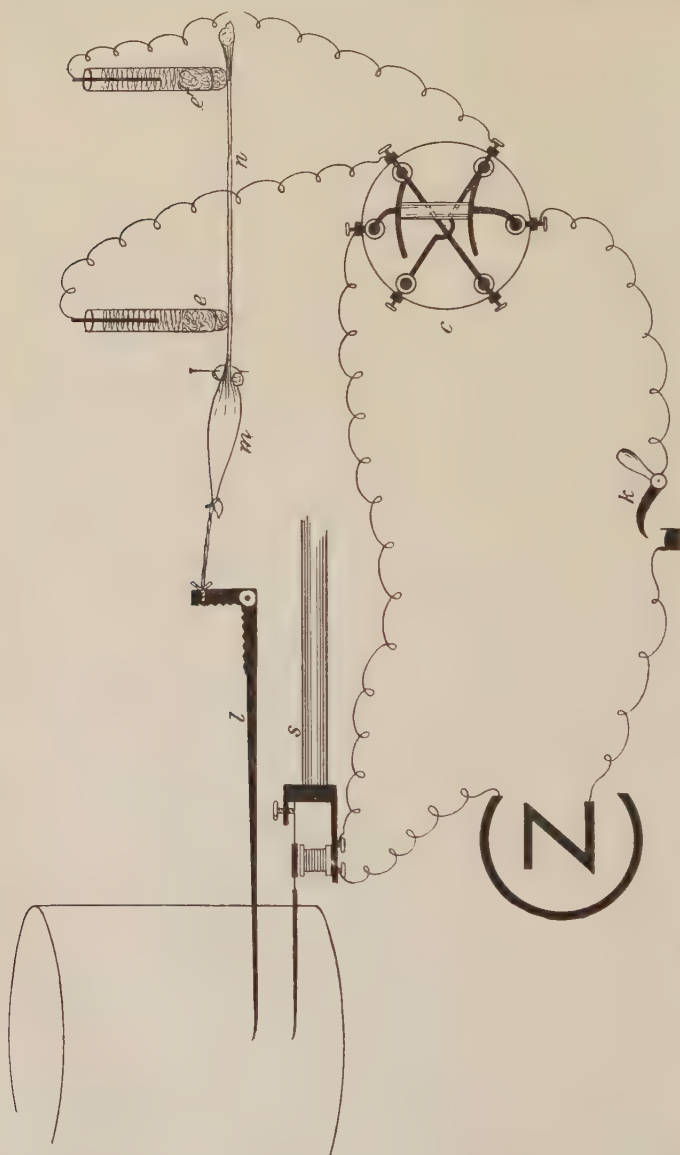


FIG. 47.—Experiment to show the polar stimulation of nerve. *m*, muscle; *n*, nerve; *l*, myograph lever; *e, e'*, non-polarisable electrodes; *c*, Pohl commutator; *k*, mercury key for closing or opening battery circuit; *s*, electro-magnetic signal.

upon the nerve, as indicated by the contraction of the muscle, of making and breaking the current when it is (1) ascending and (2)

descending. Repeat the experiment, using a *moderate strength of polarising current*—i.e., with the rider of the rheochord near the end *b* of the wire. Finally the effect of a *strong current* is to be studied by eliminating the rheochord altogether. Note down in tabular form all the results obtained. The contractions of the muscle need not be recorded graphically.

If the nerve is very excitable¹ the muscle may remain in contraction during the whole time of the passage of a strong descending current (*closing tetanus*), and may also remain contracted for a considerable time after the removal of a strong ascending current (*Ritter's opening tetanus*).

Galvanic stimulation in man.—Similar results to those obtained

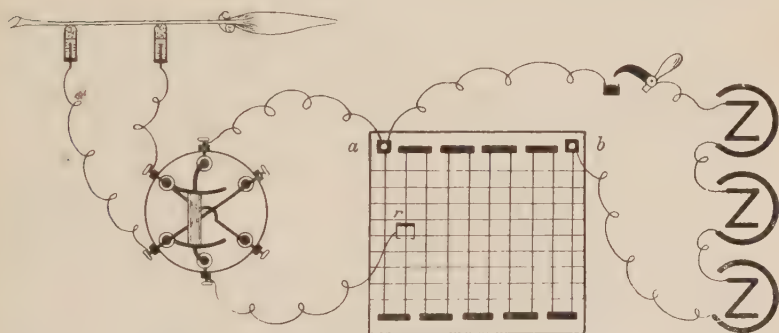


FIG. 48.—To test Pflüger's "Law of Contraction."

upon the frog's muscle-nerve preparation are obtained on closing or opening galvanic currents in the human limbs, although they are somewhat modified by the fact that the nerves to be tested are embedded in the tissues and that the human body offers great resistance to the passage of the current, so that it is necessary for obtaining some of the results to use a battery of as many as 30 or 40 cells. It is usual to employ one large-surfaced flat electrode, which generally takes the form of a zinc disc covered with flannel soaked in strong solution of salt, and is applied on the neck or sternum, and a smaller rounded electrode similarly covered and applied over the nerve or muscle to be tested. This (active) electrode is either the kathode or the anode according to the direction of the current, which may be altered at will by a

¹ The excitability of a muscle-nerve is much increased when the preparation is made from a frog which has been in a cold place or in contact with ice, and then kept for half an hour at the ordinary room temperature before being killed,

commutator. When it is a kathode, and contraction of the muscle is obtained on closing the current, the result is described as a kathodic closing contraction (KCC); when it is an anode, and contraction results from closure, it is an anodic closing contraction (ACC). Similarly the terms kathodic opening contraction (KOC) and anodic opening contraction (AOC) are employed to express corresponding results. The strength of the current is expressed in milliampères.¹

¹ The character and sequence of the anodal and kathodal muscular response as the current is strengthened is of diagnostic value in conditions of nerve-degeneration from disease. Thus while in health the sequence is KCC > ACC > AOC > KOC, at a certain stage of degeneration KCC may no longer be the most easily elicited, and the responses generally may be sluggish.

CHAPTER XII

Polar Effects of a Galvanic Current; Electrotonus

A POLARISING current, as already explained, produces changes of excitability not only at its poles but also in the adjacent parts of the nerve, and even some distance from them. This is due to the fact that owing to spread of current in the extra-polar regions changes of potential are manifested in those regions during the passage of the current between the poles, and are accompanied by physiological changes, viz., increased excitability near and beyond the kathode, and diminished excitability near and beyond the anode. Such a condition is known as *electrotonus*;

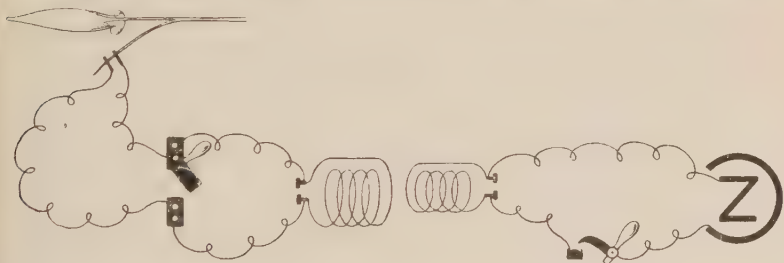


FIG. 49.—Paradoxical contraction shown by induced currents.

that produced by the kathode being termed *katelectrotonus*; that produced by the anode, *anelectrotonus*.

The spread of the electrical changes beyond the poles is illustrated by the following experiment.

Paradoxical contraction.—Dissect out the sciatic nerve of a frog, cutting all the branches save that to the calf muscles, but leaving the cut branch to the peronei muscles as long as possible. Place the cut end of this branch upon non-polarisable electrodes connected with a battery and rheochord and have a mercury key in the circuit. On making or breaking the circuit the gastrocnemius will contract. Owing to the electrotonic spread of the current in the fibres of the peroneus nerve the fibres to the gastrocnemius in the trunk of the

sciatic become stimulated; in an excitable preparation this will occur even with very weak currents. The experiment can also be performed with ordinary metallic electrodes connected with the secondary coil of an inductorium (Fig. 49). On stimulating the peroneus nerve by closing the mercury key the gastrocnemius is made to contract. If the peroneus branch is tied or crushed near its junction with the sciatic the effect can only be got with currents strong enough to spread in the tissues generally. The experiment should be repeated by placing a thread, wetted with Ringer, along the sciatic nerve, and laying its free end on the electrodes. In this case the excitation, which is, of course, caused by spread of current, will only show itself

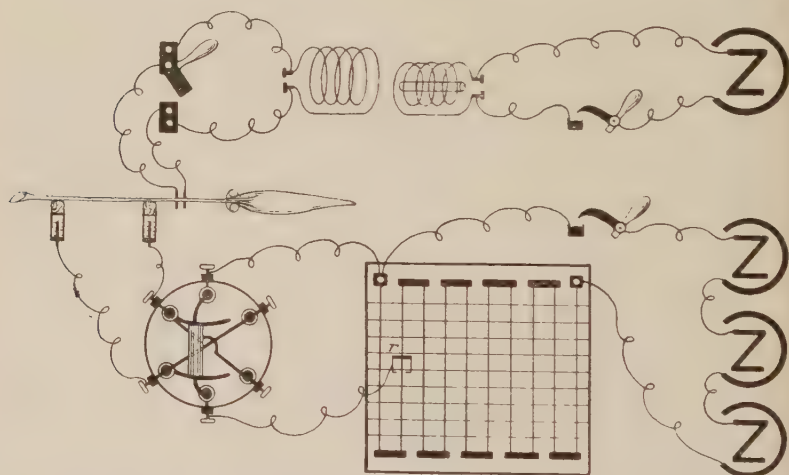


FIG. 50.—To test the polar effects of a constant current on nerve excitability.

with strong currents. These experiments show that the spread of current is assisted by the structure of the nerve; even with a weak current it takes place for a considerable distance along an intact nerve, but it is easily blocked if the nerve is tied or crushed.

Electrotonic effects of constant current on excitability.—Take a pair of non-polarisable electrodes and connect with a battery of at least two cells, inserting a rheochord, a commutator, and a mercury key into the circuit (*polarising circuit*). Another circuit is also prepared (*exciting circuit*), including cell, induction coil, and mercury key in connection with the primary coil; the secondary coil is furnished as usual with a short-circuit key, with which a pair of ordinary metallic electrodes are connected; these electrodes are brought in

contact with the nerve of a muscle nerve preparation *near the muscle*. Be careful to keep the nerve moist. The non-polarisable electrodes, which may be of the boot pattern, are slightly raised above the myograph cork: they must not be allowed to be short-circuited by the Ringer solution used to keep the preparation moist; the upper part of the nerve is laid upon them (Fig. 50). The record of the muscular contractions obtained is made on a stationary drum.

Place the secondary coil at such a distance from the primary coil that faradisation (Helmholtz modification) just produces a small contraction. Now put in the polarising current (1) in an ascending and (2) in a descending direction, and determine the effect of its poles in diminishing or increasing the excitability of the nerve as tested by the height of the ordinates described by the myograph lever.

This experiment can be performed without taking a graphic record by noting at what distance the secondary coil must be placed in order just to produce a contraction. In this way the varying conditions of excitability produced by the polarising current may be recorded numerically.

A variation of the experiment is to replace the exciting circuit by a few crystals of salt and wait until the penetration of this begins to excite the nerve fibres.

The rheochord may be dispensed with in the polarising circuit.

CHAPTER XIII

Experiments on the Electrical Conditions of Muscle and Nerve

A GALVANOMETER or electrometer is necessary to study these conditions, but certain facts can be demonstrated without any special apparatus.

Demarcation current of muscle: Contraction without metals.—By means of a glass rod, loop up the nerve of a nerve-muscle preparation and allow its cut end to come in contact either with an injured part of the surface of its own muscle (Fig. 51) or with other muscles. There will be a contraction of its muscle each time that the contact is made or broken. The excitation is caused by the passage through the nerve of part of the demarcation current of the muscle.

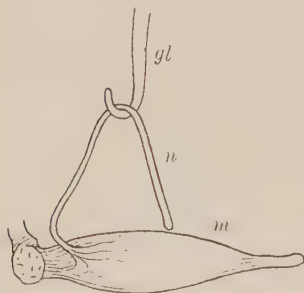


FIG. 51.—Experiment of the contraction without metals.
gl, bent glass rod; *n*, nerve;
m, muscle.

The result can sometimes be obtained if the cut end of the nerve is allowed to touch a part of the nerve nearer the muscle: in this case it is the demarcation current of the nerve which stimulates its own fibres.

This experiment is only likely to succeed if a very excitable preparation, such as is obtained from a cooled frog (see footnote, p. 59), is employed.

Action-current of muscle; Secondary contraction.—Take a nerve-muscle preparation, and lay its nerve over another nerve-muscle preparation, the nerve of which is placed upon electrodes (Fig. 52). Tetanise this nerve; the nerve of the first-named preparation will be stimulated by the electrical variations which accompany the contraction of the tetanised muscle. A nerve-muscle preparation thus used in place of a galvanometer to indicate electrical variations is known as a *rheoscopic frog preparation*.

The result can also be obtained with single excitations.

Secondary contraction from the heart. Lay the nerve of a muscle-nerve preparation upon the beating heart of the frog. If the preparation is very excitable the muscle will twitch with each beat of the ventricle. If the heart-beat and the twitch are simultaneously recorded on a drum the twitch will be found to slightly precede the beat—*i.e.*, the electrical change precedes the mechanical; this is seen best with a cooled heart.

Measurement of demarcation current; Capillary electrometer.—The capillary electrometer consists of a thread of mercury, which is forced by pressure from behind for a certain distance along a glass tube drawn out to a capillary termination; the free end of the capillary is filled with dilute sulphuric acid and dips into a vessel containing the same fluid. The capillary is observed with a microscope. If the

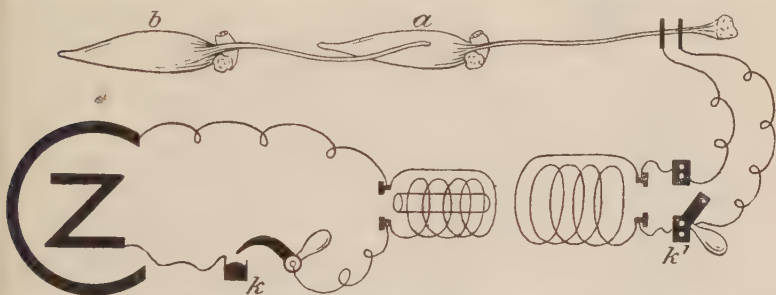


FIG. 52.—Experiment to show secondary contraction. *k*, mercury key in primary circuit; *k*¹, short-circuit key in secondary circuit; *a*, first muscle; *b*, second muscle with its nerve laid over the first.

mercury and the sulphuric acid are now connected with wires which are charged with electricity, there is produced a movement of the mercury in the direction which the current would take—*i.e.*, from positive to negative—the extent of movement through a small range being, for the same electrometer, proportional to the difference of potential. From the direction and extent of the movement the direction and electromotive force of any constant current may therefore be gauged. The movements of the meniscus can be photographed, and a graphic record thus obtained. The sensitiveness of the capillary electrometer may be greatly increased by the introduction of thermionic valves (Adrian).

Join a pair of non-polarisable electrodes up in circuit with a capillary electrometer and Daniell cell through a rheochord and commutator in the manner shown in the diagram (Fig. 53), but with a piece of blotting-paper moistened with salt solution placed across the electrodes instead of the muscle shown in the figure. Have the short-circuiting key (*k*¹) shut at first (so that the electrometer is short-

circuited), and the battery key (*k*) open. Bring the mercury meniscus into the field of the microscope. Now open the short-circuiting key. If the electrodes are themselves without current there will be no effect on the electrometer; but usually there is a slight effect, the direction and the amount of which should be noticed. Next close the battery circuit, leaving the short-circuiting key open. Part of the battery current is now sent through the electrodes and electrometer in a particular

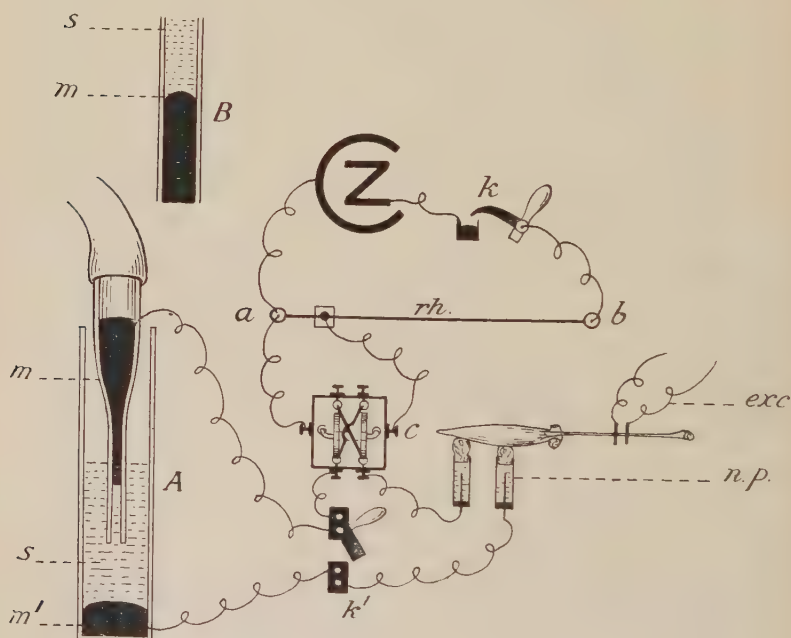


FIG. 53.—Diagram of capillary electrometer. *A*, reservoir containing sulphuric acid, *s*, and mercury, *m'*; *m*, mercury in glass tube drawn out to capillary termination; *n.p.*, non-polarisable electrodes; *exc*, exciting electrodes; *k*, *k'*, keys; *c*, commutator; *rh*, rheochord; *B*, capillary as seen under microscope.

direction (which can be reversed by the commutator), and there is a corresponding movement of the mercury. Note the direction of this movement, and by following out the wires from the battery determine with which part of the electrometer the anode and kathode are respectively connected. By means of the rheochord and commutator a definite portion of the battery current can be sent in either direction through the electrodes and through any preparation with which they

may be connected. Open the battery key and close the short circuiting key; the meniscus should return to its original position.

Lay the muscle of a nerve-muscle preparation, which may have the distal end cut or injured, upon the electrodes in place of the wet blotting-paper. Place it with one electrode touching the longitudinal surface and the other at or near the injured end. Then open the short-circuiting key to allow the *demarcation current* of the muscle to affect the electrometer. From the direction of movement of the mercury determine the direction of the muscle current through the apparatus—*i.e.*, which part of the muscle led off from the electrodes is negative to the other. The electromotive force of the current can be measured by closing the battery key, so that the battery current is brought into the circuit, and by aid of the rheochord and commutator sending a current through the circuit in a direction the reverse of the demarcation current and of exactly such a strength (measured by the known electromotive force of the battery employed and the position of the rider on the rheochord) as to bring the mercury back to zero.

Action current.—Place the upper end of the nerve of the preparation on a pair of exciting electrodes (*ecc*) connected with an induction coil arranged for tetanisation. Observe the meniscus with the microscope, and tetanise the muscle, using the weakest possible stimulus. Notice that the meniscus moves in a particular direction.

This movement is caused by a change in the electrical condition of the muscle accompanying its contraction. From the direction of movement of the mercury determine which part of the muscle is now negative to the other. The action current can only be properly studied in photographs of the end of the mercury column, the image of which is thrown on a slit in front of a moving photographic plate.

String galvanometer of Einthoven.—This consists of a microscopically fine thread of silvered quartz or of wire stretched between the poles of a powerful electro-magnet (Fig. 54). When a galvanic current is passed along it the thread is deflected to one side or the other to an extent varying with the E.M.F.—the tension of the thread being supposed constant. The movement is observed with a microscope, or the mag-

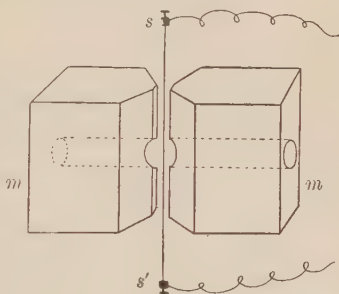


FIG. 54.—Diagram of Einthoven string galvanometer. *s, s'*, wire or silvered quartz thread, stretched between the two poles of a powerful electro-magnet, *m, m*, which are perforated to allow a microscope to bear upon the thread.

nified image of the thread is photographed on a moving sensitised surface. The method of conducting the experiment is very similar to that employed for the capillary electrometer. For certain investigations, especially those relating to the electrical conditions accompanying the action of the heart, the string galvanometer is more convenient than either the capillary electrometer or the needle galvanometer. It has been largely adopted by clinicians, since the heart-records obtained by it (electro-cardiograms) furnish valuable indications

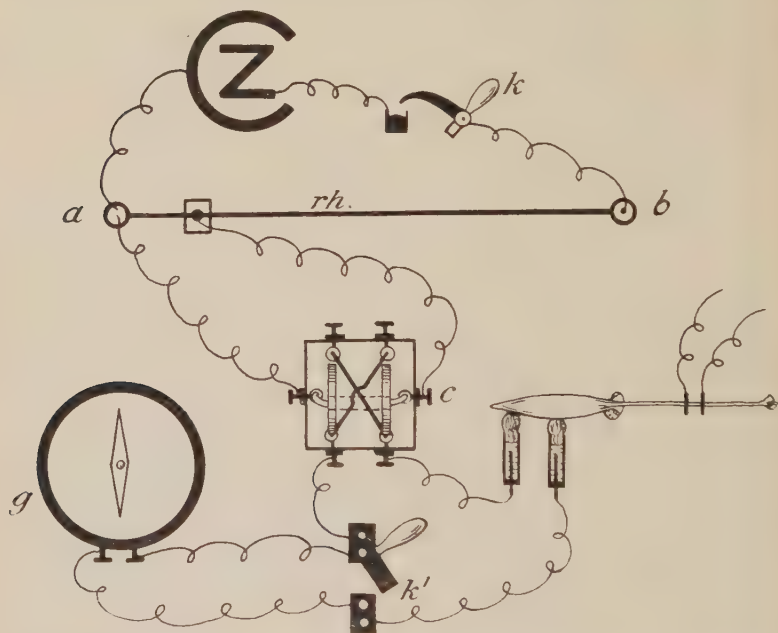


FIG. 55. --Diagram of arrangement of apparatus for studying muscle currents with galvanometer. *g*, galvanometer. The other letters as in Fig. 53.

as to the nature of cardiac affections which might be otherwise difficult to diagnose. When used for the human subject the two hands, or the right hand and left foot, are placed in vessels of salt solution, and these are connected, by a suitable non-polarisable arrangement, with the ends of the quartz thread or wire.

Reflecting needle galvanometer.---Reflecting galvanometers of high resistance were, until recent years, almost exclusively used for experiments in electro-physiology (Fig. 55), but have been largely superseded by the instruments that have just been described.

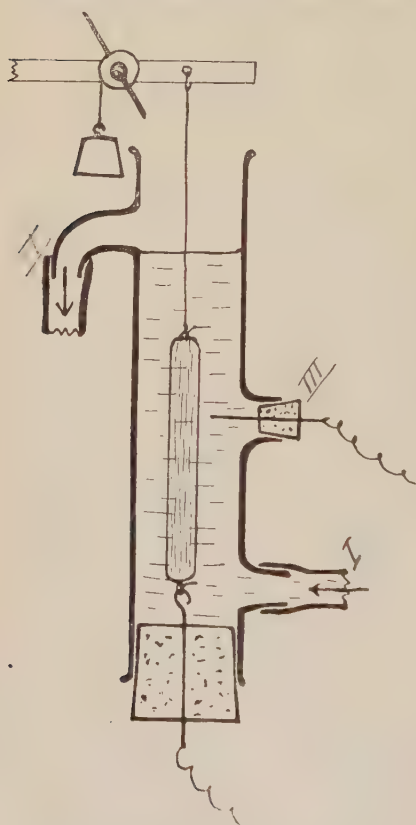
Demarcation and action currents of nerve.—These are examined and measured in exactly the same way as those of muscle.

Action current of frog-heart.—Non-polarisable electrodes are connected with a beating frog-heart, which may either be removed from the body and laid with the base upon one electrode and the apex on the other, or left *in situ*, and the electrodes connected with apex and base by thick threads wetted with salt solution. The electrodes are joined by wires to any of the above instruments. Each contraction of the heart is accompanied by movements of the respective indicators (mercury column, silvered quartz thread, or magnetic needle), the deflections of which are recorded and the alterations in electrical potential of base and apex deduced therefrom.

CHAPTER XIV

Involuntary Muscle

Stomach or bladder of frog.—Take either a transverse strip from the



stomach—the frog should have been recently fed—or the whole urinary bladder, fastening a thread to each end. For recording the contractions, which may be spontaneous and rhythmic, or may need to be elicited by excitation, the apparatus shown in Fig. 56A is employed. This consists of a glass tube of the size and construction shown in the diagram. One end of the preparation is tied securely to a hooked wire passing through a cork, which closes the lower end of the tube, and serves as an electrode, whilst the other end is attached by a thread, passing through the open upper end of the tube, to the short arm of a very light lever. The tube has three lateral openings; one, near the bottom for inflow of fluid, a second near the top for outflow, and a third, closed by a cork, through which a wire is passed to serve as a second electrode. The glass tube is filled with Ringer's solution. Bring fine wires from a battery of two or three Daniell cells through a simple key, placing

FIG. 56A.—Diagram of apparatus for recording the contractions of a strip of frog's plain muscle immersed in Ringer's solution, and for investigating the action of drugs and animal extracts upon the tissue.

one wire in contact with the lower, the other with the upper electrode. This upper electrode need not touch the tissue. Use a very slow drum. Stimulate by making and breaking the circuit. If induced currents are employed there is usually no response with a single make or break

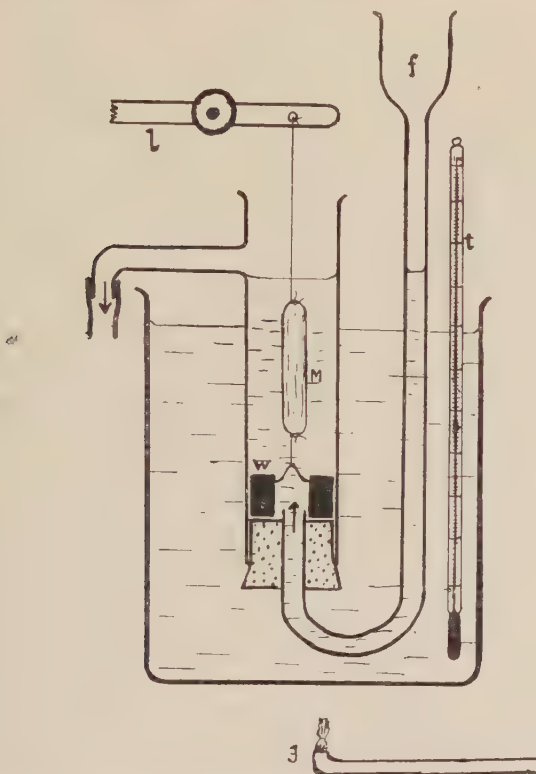


FIG. 56B.—Diagram of apparatus for investigating the contractions of mammalian plain muscle and the action of drugs and extracts upon it. *M*, muscle within experimental tube filled with Locke's solution. The strip of muscle is attached below to a leaden weight, *w*, and above to a lever, *l*. A bent glass tube terminating in a funnel, *f*, serves to introduce fresh Locke, containing a known percentage of the drug, into the tube, displacing the normal Locke. *g*, gas-jet; *t*, thermometer.

of the primary circuit owing to the short duration of the induction shock, but by repeating the stimulus the tissue will contract and the lever will describe a simple prolonged muscle curve on the drum. The contraction may also be obtained by a rapid succession of induced

currents, using the Neef's hammer, but it is always a simple contraction, not a tetanus.

Intestine of rabbit: Magnus' method.—A similar apparatus (Fig. 56B) is used, but the experimental tube, filled with Locke's solution (footnote p. 2), must be kept at 35° C. For this purpose it is immersed in a beaker of water maintained at this temperature by a gas jet. A longitudinal piece of rat's or rabbit's small intestine, or a short strip of the longitudinal muscular coat of the small intestine of the dog or cat, is attached below to a leaden weight resting on the cork and above to the lever. After a short time rhythmic contractions occur and should be recorded. For prolonged experiments oxygen is allowed to bubble through the Locke so as to keep the solution saturated with this gas.

This method is particularly useful for investigating the action of drugs and autacoids upon plain muscular tissue. The Locke solution containing the substance to be tested is placed in a test tube in the warm bath, and, after a normal tracing has been made, the Locke solution in the experimental tube is replaced by that containing the drug or extract by pouring the latter into the funnel (*f*) and letting it displace the normal Locke. In the same way a normal solution, warmed to the same temperature, can be made to displace that containing the drug or extract. In this manner it can be determined in the case of intestinal muscle that the effect of adrenaline is inhibitory (chalone), restraining the contractions and tone: that of barium excitatory (hormonic), increasing the contractions and tone.

Uterine muscle.—The movements of the uterus may be recorded by this apparatus by taking a piece of one of the uterine cornua of a rat or guinea-pig and fixing it in the same way in the experimental tube. The effect of pituitary extract in increasing the contraction may be readily demonstrated on such a preparation.

CHAPTER XV

The Frog-Heart

Dissection.—Make a special dissection of a large frog to show the situation and connexions of the heart, its several cavities, and the blood-vessels leading to and from it. It is advantageous to distend the cavities with gelatin solution and allow this to set. Notice a small nerve entering the heart on each side along the superior vena cava; this is the cardiac nerve, and is given off from the vagus; it contains also fibres from the sympathetic which reach the vagus near the skull. Cut out a piece of the interauricular septum; place it in

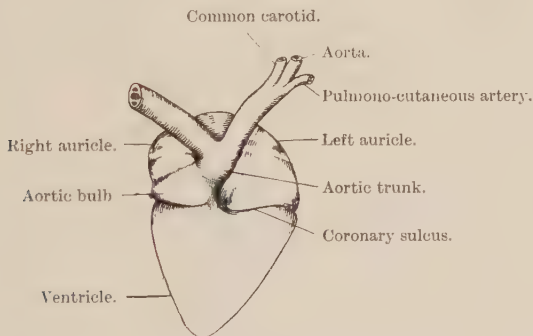


FIG. 57.—Heart of frog; ventral aspect (Gaupp).

very dilute methylene blue for five minutes; wash with water, and examine in water under the microscope for nerve-fibres and groups of nerve-cells. The dissection of the heart may be made beforehand and kept for reference in dilute formalin.

Experiments.—Examine the contracting heart of a frog, the brain and spinal cord of which have been destroyed; cut away the sternum and ensiform cartilage and the front of the pericardium. Very gently raise the tip of the ventricle with a blunt instrument, and sever the pericardial ligament which binds the ventricle to the back of the peri-

cardium. *Do not grasp the heart with forceps or injure it in any way by manipulation.*

On raising the ventricle the sinus venosus comes into view, receiving the two venæ cavæ superiores and the vena cava inferior. Above,

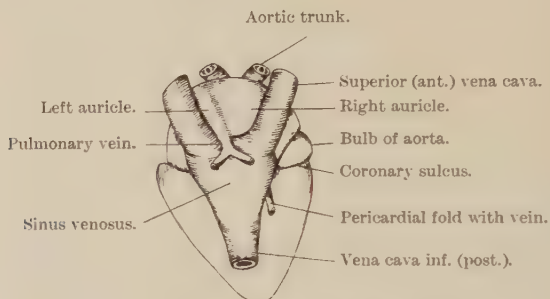


FIG. 58.—Heart of frog from dorsal aspect (Gaupp). $\frac{2}{1}$.

the sinus is continuous with, but marked off by a whitish line (sinus-auricle junction) from, the auricle, which is double and receives on the left side the pulmonary vein: the two auricles open into a single ventricle. On the front the bulbus aortæ is seen leaving the

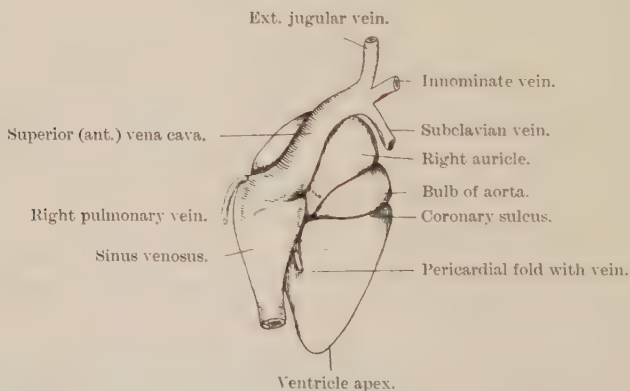


FIG. 59.—Heart of frog, seen from the right side (Gaupp). $\frac{2}{1}$.

ventricle and dividing into two trunks, the right and left aortæ, each of which again soon divides into three branches.

Notice that with each systole the venous part of the heart (sinus venosus) contracts first; its contraction is immediately followed by that of the auricles, which contract together, and this by that of the

ventricle. In a frog the spinal cord of which has been destroyed there is usually little or no blood passing through the heart. But if blood is being pumped through, notice the sudden distension (diastole) of each cavity which immediately succeeds its contraction (systole).

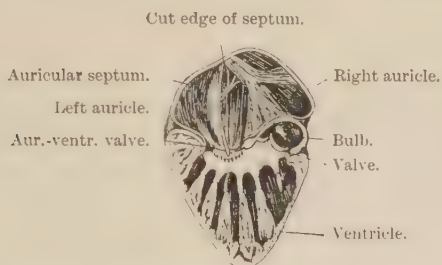


FIG. 60.—Section through heart of frog. Front half seen from behind (Gaupp). The spongy structure of the ventricle is shown. $\frac{2}{4}$.

If the finger is very lightly placed on the ventricle the hardening which accompanies systole may be felt (cardiac impulse).

Effect of heat and cold on rate of beat.—Using a watch, count the number of beats per minute during several minutes and record the average. Now apply, first, an ice-cold and, second, a warmed copper

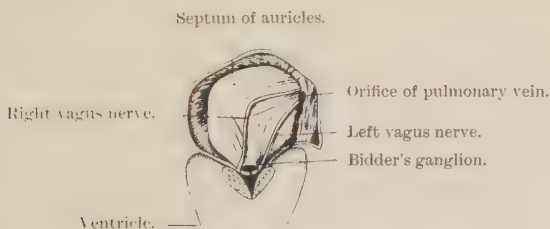


FIG. 61.—Heart of frog with left auricle cut open to show the vagus nerves in the auricular septum (Gaupp). $\frac{2}{1}$.

rod (*a*) to the ventricle, (*b*) to one of the auricles, and (*c*) by turning up the heart, to the sinus. Count the rate immediately after each application, and note down the results.¹

¹ The effects of heat and cold, and also those produced by the Stannius ligatures, can be recorded by attaching the heart to a light lever (as in Fig. 62); but they should always in the first instance be investigated without the use of any mechanical appliance.

Stannius' experiment.—Raise the ventricle very carefully without pinching or injuring it in any way, and, after cutting the ligament or fold of pericardium before mentioned, which encloses a small vein, pass a thread under the sinus, and tighten it round the sinus-auricle junction. The sinus continues to beat as before (count the rate), but the auricle and ventricle usually come to a standstill in diastole. Such a heart is termed a *Stannius heart*.

Gently prick auricle or ventricle, and notice that each stimulation is followed by a contraction starting from the point of stimulation and spreading to all parts of auricles and ventricle. They are therefore not inhibited (prevented from contracting), but have ceased to contract owing to their being cut off, by the ligature, from the sinus, in which the contractions normally begin.

Now tie a second ligature round the auriculo-ventricular junction. The ventricle usually gives three or four beats, and then both it and the auricle again come to a standstill. Either can, however, be made to beat by artificial stimulus (prick, electric shock).

After a certain lapse of time (sometimes very soon after the application of the first ligature) the auricle and ventricle may recommence beating regularly and rhythmically, but it will be found on counting the rate that it is never as fast as that of the sinus. If the auricle is cut off from the ventricle, as by the second Stannius ligature, all three parts may ultimately be found beating spontaneously, but it will always be noticed that the rate of the sinus is the fastest, that of the auricles next, and that of the ventricle the slowest. The bulbus aortæ is also spontaneously contractile; even small pieces can be observed to beat rhythmically.

Peculiarities of cardiac contraction.—Apart from its regular spontaneous rhythm the heart-muscle shows certain phenomena, which are not peculiar to it, but are much more strikingly exhibited than by skeletal muscle. To investigate these it should be used as a muscle, the spontaneous contractions being eliminated as follows:—

Apply a ligature at the base of the ventricle; cut out the heart and attach the apex by means of a very fine hook and thread to a very light muscle lever (such as is shown in Fig. 62), the preparation being fixed by a pin passed through the ligatured base. Or the heart may, if desired, be left *in situ* as shown in the figure; in this case also its base must be fixed to the cork by a pin. *Be very careful not to injure the heart.* Contractions are recorded by the lever in the same way as those of any other muscle. Use a very slow drum (one revolution in 5 minutes). As a rule there are no spontaneous contractions of the ventricle, but it responds to a stimulus applied to any part of its surface.

Allow a pair of electrodes, connected with an induction coil, to touch the base of the quiescent heart. They must be fixed (this can be done with plasticine), not held in the hand. The following experiments may now be made:—

1. **Staircase phenomenon** (see p. 49).—Use the above “Stannius” preparation, and a very slowly moving drum; or the drum may be stationary during the record, and moved about 5 mm. by hand between the stimulations.

After a period of rest, put in single maximal stimuli at intervals of about two seconds, and record each contraction. Notice that there is a slight increase in the extent of the first few successive contractions, the second ordinate being a little higher than the first, the third than the second, and so on, but they soon become of exactly the same

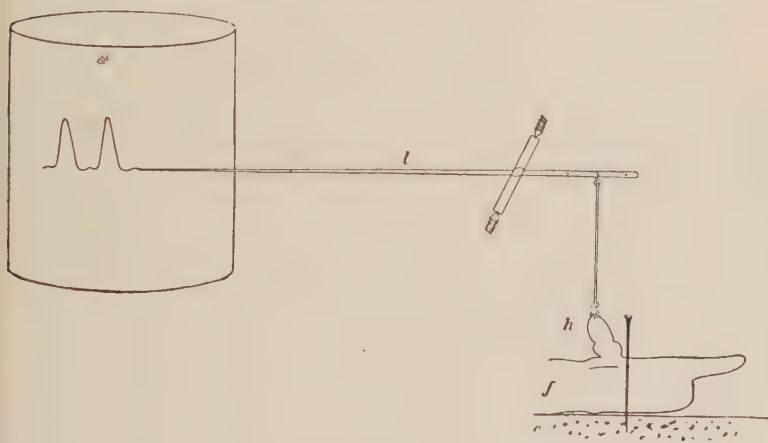


FIG. 62.—Frog cardiograph. *f*, frog; *h*, heart; *l*, lever.

height. The experiment shows that the effect of a first contraction is to increase the amount of shortening of the tissue for the contraction immediately succeeding it, and similarly for the next contraction, but only up to a certain point.

2. **Refractory period.**—For this experiment the drum must move fast enough to spread out the curve of the ventricular contraction to about 1 centimetre long. A first stimulus is put in, and during the record of the contraction caused by it a second stimulus is allowed to follow it at varying intervals after the first. Mark the moment of putting in the second stimulus by a dot on the curve. If the second comes soon after the first, so as to reach the heart whilst it is still in process of contraction, no additional effect is produced; there is *no super-*

position (compare with skeletal muscle, p. 41). In other words, whilst the contraction produced by the first stimulus is actually proceeding, cardiac muscle is entirely *refractory* to a second stimulus. This refractory condition is continued in a modified degree during the period of relaxation of the muscle. A consequence of the long refractory phase and of the lack of superposition is that *cardiac muscle never shows a true tetanus*, although by sending in successive stimuli so that they reach the muscle always at the commencement of the period of relaxation, there is an appearance of fusion of the successive contractions: but they never overtop one another as in tetanus of skeletal muscle.

The existence of a refractory period can be observed by exciting the exposed frog-heart whilst beating normally *in situ* and without attaching it to a lever.

3. "**All or none**" contraction.—Put the secondary coil far from the primary, and excite the preparation by breaking the primary circuit. Determine the excitability by ascertaining to what division of the scale the secondary coil must approach the primary before a contraction is produced. This represents the *liminal stimulus*. Now bring the secondary nearer the primary and again stimulate. The contraction is not appreciably larger. Repeat with stronger and stronger stimuli: lastly, repeat with diminishing strength of stimulus. Apart from the "staircase" effect already studied, in every case the extent of contraction (if any) is the same. The case is different with skeletal muscle. This difference is connected with the fact that the individual fibres of skeletal muscle contract independently of one another, and with the stronger stimuli a greater number are thrown into contraction.

CHAPTER XVI

Perfusion of Heart

Perfusion of frog-ventricle.—Kill a large frog and expose the heart ; remove the pericardium and cut through the pericardial ligament. Very carefully raise the apex of the ventricle with a blunt instrument, remembering that the least injury to the surface of the ventricle will spoil it for this experiment. Make a free cut with scissors into the auricles thus exposed, near to the sinus-auricle junction ; insert the scissors into the auricles and snip through their septum. Wash all blood away with Ringer's solution. Place a ligature of wet cotton round the auricles near their junction with the ventricles ; insert the double perfusion cannula (Fig. 63, *f*) through the auricles and into the ventricle, and tie it in firmly by means of the ligature ; cut through the sinus, and remove the heart upon the cannula. The inlet tube of the perfusion cannula is connected with a reservoir (Mariotte bottle) containing about 100 c.c. Ringer's solution, and the outlet tube conducts to a receptacle into which the fluid may flow after passing through the heart. Whilst the heart is being fastened over the cannula, let Ringer's fluid flow very slowly (drop by drop) through the cannula so as to expel and keep all air out of the cannula and heart.

Now place the heart in the plethysmograph (Fig. 63). The lower part of the plethysmograph contains Ringer's solution ; the upper part and the tubes leading horizontally from it contain pure, moderately thin paraffin oil.¹ Both stopcocks are closed whilst the heart is inserted ; then the one belonging to the bent tube is opened. If the reservoir of Ringer's fluid is at a height of three or four inches above the heart, the ventricle will soon begin to beat, and its changes in volume will cause a movement of the oil to and fro in the open tube. If this tube is now closed and the one containing the piston opened, the piston will move to and fro, and its movements can be recorded on a very slowly rotating horizontal drum.

¹ Not olive oil. Ringer's solution may be substituted for oil in the plethysmograph itself, but for the piston-tube oil is required.

If the tube *g* is vertical instead of horizontal the apparatus can be employed with a vertical drum, but the piston must fit very accurately.

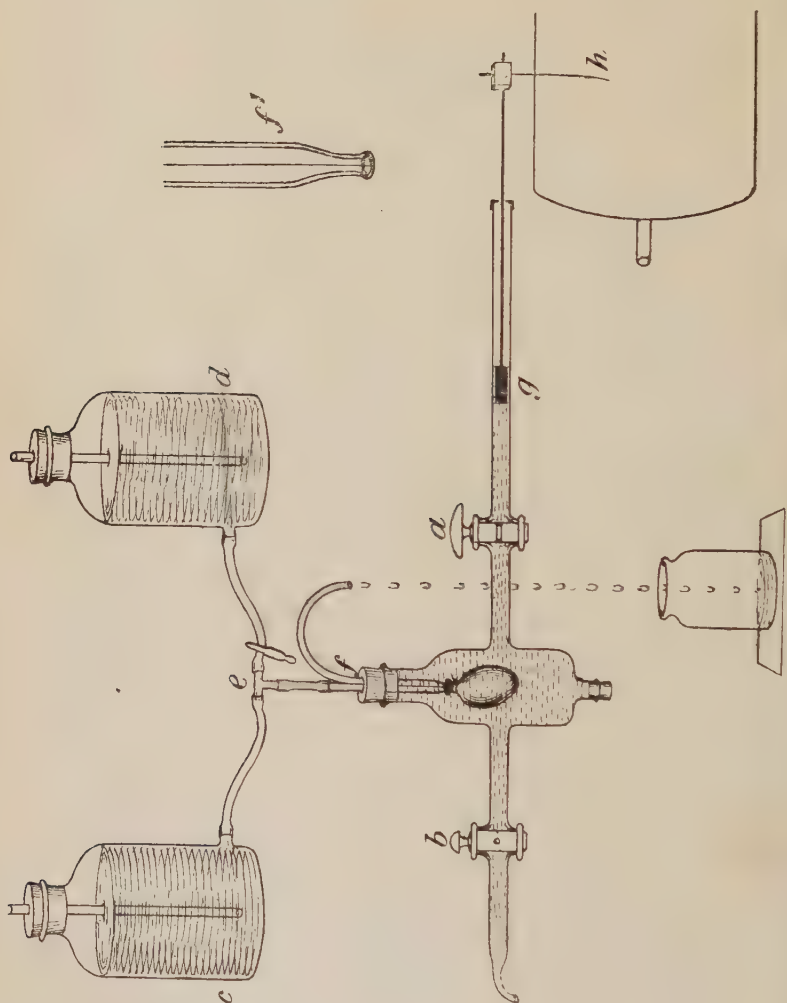


FIG. 63.—Frog-heart plethysmograph. *a*, *b*, taps; *c*, *d*, Mariotte bottles; *e*, three-way tube; *f*, Kronecker cannula; *f'*, end of cannula enlarged; *g*, piston (this can be made of hard rubber).

It may happen that the perfused heart (which is a Stannius heart) does not begin to beat spontaneously, although the salts and the pressure of fluid serve as a slight stimulus. In that event the beats may be started by faradic excitation from an induction coil, one

electrode being attached to the metal cannula and the other to a wire which passes up through a cork in the bottom of the plethysmograph, and is brought in contact with the ventricle.

The influence of various ions such as calcium and potassium can be studied by adding definite amounts of their salts to the Ringer's solution used for perfusion. For many purposes it is convenient to

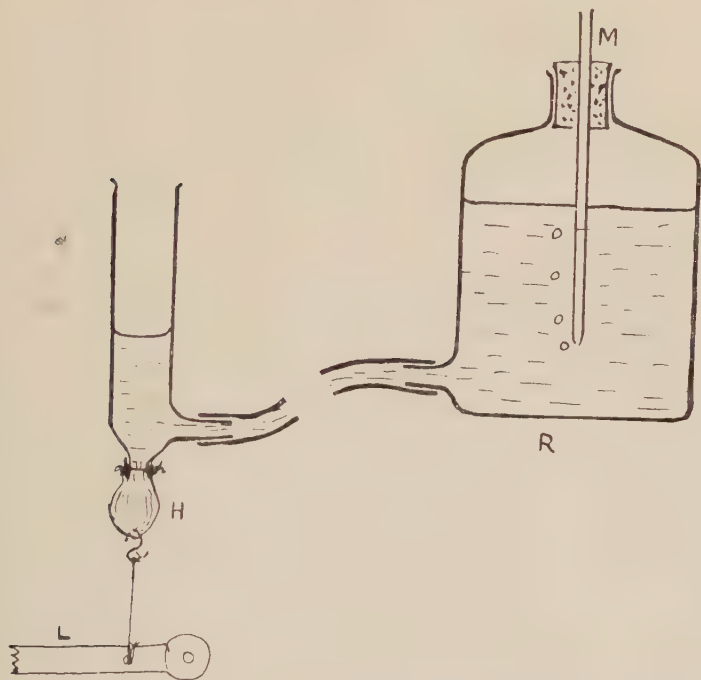


FIG. 64.—R, reservoir (of Ringer's solution) connected with heart cannula by india-rubber tubing provided with a screw-clip (not shown in the diagram); M, Mariotte-tube for maintaining a constant pressure; H, heart tied to cannula and connected by fine hook and thread to lever, L.

have two reservoirs of Ringer's solution (Fig. 63), one for addition of the substance to be investigated, and the other to flush out the heart after the action of the substance has been determined. Both reservoirs are connected with the inflow of the cannula by a three-way tube (*e*) furnished with a stopcock or with small clips.

In this way the effects of drugs and animal extracts may

be investigated; one reservoir containing pure Ringer solution, the other Ringer containing a known amount of the drug.

Influence of calcium and potassium on the cardiac contractions: Ringer's experiment.—Place in the second reservoir a solution containing six parts of pure NaCl to 1,000 of distilled water, and keep it filled with this solution. Flush the heart with it; the organ will soon cease to contract and to respond to excitations. Now mix with the 100 c.c. of fluid in the second reservoir 1 c.c. of a 1 per cent. solution of calcium chloride and flush the heart with the mixture. Contractions will be resumed, but each one will be too prolonged, and the heart will again soon stop: this time in systole. Next add 0.75 c.c. of a 1 per cent. solution of potassium chloride to the contents of the second reservoir, mix thoroughly, and flush the heart with the mixture. The beats will recommence, either spontaneously or in response to stimulation, the normal character being resumed. If the potassium salt is added in excess the heart will be arrested in diastole.

Perfusion of the whole heart (Fig. 64).—For this purpose a wide glass tube, open at the upper end and terminating below in a cannula, is used: there is a short lateral tube near this end. The cannula is introduced into the sinus venosus and tied in. The heart (H) is then completely cut out from the body, and the tube is fixed vertically to a stand, the apex of the ventricle being attached by a hook and thread to a light lever (L). The lateral tube of the cannula is connected with a Mariotte bottle of Ringer's fluid (R). The heart is perfused with the solution, which drops from the cut aorta into a suitable receptacle (not shown in the diagram) placed below the lever. Drugs are introduced either by means of a second bottle, as in Fig. 63, or by injecting them into the vertical tube by a hypodermic syringe or fine pipette.

Perfusion of the mammalian heart.—The heart is excised from a recently killed cat or rabbit, and the aorta is at once tied on to a cannula through which Locke's solution, saturated with oxygen, is slowly dropping. The solution is warmed, before reaching the heart, by being passed through a glass spiral in a water bath heated to about 38° C. The heart should itself be enclosed in a warmed chamber. The cannula is directed towards the aortic valves, which are closed by the pressure (about 80 mm. Hg.) of the perfused fluid; this runs through the coronary vessels and escapes through the right auricle. The amount of fluid perfused can be measured by a tilter (see Fig. 80). The contractions are recorded by light levers, attached to auricle and ventricle by threads which are passed round pulleys (Fig. 67).

The action of drugs and autacoids is investigated by adding them to the Ringer's solution. The best way to introduce them is to inject them with a hypodermic syringe into the rubber tubing which conducts the Ringer's fluid to the heart.¹

¹ For a more detailed description of this method of perfusion, the student should consult Sherrington's *Mammalian Physiology*.

CHAPTER XVII

Cardiac Nerves of Frog

DESTROY by a wire the spinal cord of a frog, and also remove the cerebral hemispheres; this can be done without special dissection by cutting away with a razor the upper jaw and anterior part of the skull at the level of the front of the tympana (see Fig. 84, p. 121). The posterior part of the brain with the medulla oblongata must not be injured. Fix a pair of pin-electrodes connected with an induction coil into this part of the skull and arrange for tetanisation of the medulla oblongata—using the Helmholtz method (p. 17). Lay the frog upon its back on the frog-cork, and fix it securely by strong pins; expose the heart and the chief nerves which are proceeding from the base of the skull to the hyoid region (vagus, glosso-pharyngeal, and hypoglossal; see Fig. 65). The vagus gives off a small branch on each side, which runs close along the superior vena cava to the sinus venosus. Place one vagus trunk upon a fine pair of wire electrodes (which must be fixed by plasticine to the frog-cork, not held in the hand), and connect these electrodes, and also those which are fixed into the skull, to a commutator without cross wires so that the faradising shocks can be sent to one or other pair as may be desired. Place the cork below the lever of the frog-cardiograph, and by means of a thread and fine hook attach the apex of the ventricle to the short arm (Fig. 62). Record the contractions of the heart upon a very slowly moving drum (one revolution in five minutes). Use the “stop” for adjusting the lever and for readjusting it after removal from the drum, so that the pressure of the lever point is always exactly the same. Without this precaution the strength of the contractions may be wrongly judged, for if the lever is pressing more at one time than at another, the lever will not be raised so high, even if the force of the heart's contractions is unaltered.

Be careful not to injure the heart. In order to fix it securely, pass a strong pin close to its base and through the vertebral column into the frog-cork.

The following experiments may be performed upon this preparation:—

1. Take a normal tracing of the beats during a short period and record, by an electro-magnetic signal or by marks made by hand, a time-tracing (minutes) upon the drum. This time-tracing is to serve for determining the exact rate per minute of the heart beat under the different circumstances of the experiments.

2. Whilst the record is proceeding, stimulate the medulla oblongata, allowing the result to be traced continuously at the same level of

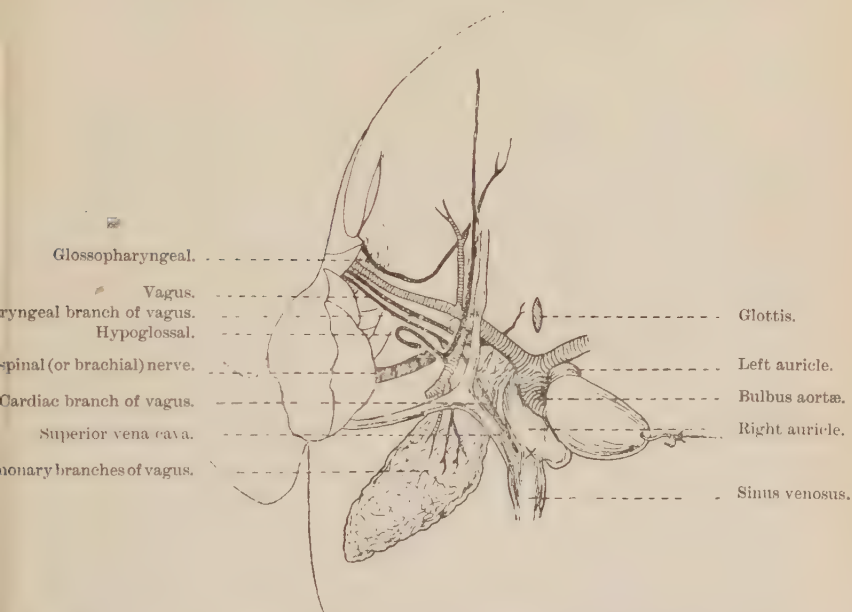


FIG. 65.—Relations of vagus nerve to other structures in the neck and thorax. The ventricle has been drawn over to the left side by a hook and the sinus venosus is thus exposed. ×, line of junction between sinus and auricles.

the drum. (The excitations must in no case be so strong as to escape to other parts of the preparation.)

3. Cut both vagus nerves a short distance from the skull and repeat the above stimulation of the medulla oblongata, recording the result at another level of the drum.

4. Alter the commutator to stimulate the vagus nerve, recording the result at a third level of the drum. With weak stimulation of the vagus in the frog the heart may beat faster and more strongly owing to excitation of the sympathetic fibres which have joined the vagus near the skull and are running with the cardiac branch to the heart ;

with stronger stimulation the heart will beat more slowly and less vigorously, or may stop altogether.

5. Place one drop of a 0.2 per cent. solution of nicotine upon the sinus. The effect of this is at first to slow the heart, because the nerve-cells to which the vagus fibres are distributed are stimulated by the drug; subsequently they are paralysed, and the heart resumes its normal rate. After a short interval stimulate the vagus. No effect should be obtained, since nicotine blocks the junction of the nerve-fibres with the distributing nerve-cells within the heart. Wash away the nicotine with salt solution; the effect will return after a time.

6. Stimulate the heart at the white line of the sinus-auricle junction. (The electrodes must not be held in the hand, but must be fixed in position by plasticine.) The heart comes to a standstill in diastole. Record this effect in a continuous tracing. This standstill is not due to the stimulation of an inhibitory centre, but to the fact that the inhibitory fibres of the vagus are close to the surface at this place.

7. Place a single drop of dilute solution of muscarine upon the sinus, recording the effect produced upon the rate and force of the heart, which will soon come to a standstill in diastole owing to the fact that muscarine stimulates the terminations of the inhibitory fibres. Now wash away the muscarine with two or three drops of solution of atropine sulphate (1 in 300). Notice the gradual restoration of the rate and force of the beats. Notice further that no inhibition can now be produced on stimulating either the vagus or the sinus-auricle junction, *i.e.*, atropine antagonises muscarine and paralyses the terminations of the inhibitory fibres. There may, however, be *acceleration*, from stimulation of the sympathetic fibres which are running to the heart in the cardiac branch of the vagus.

Notice that in each case of acceleration or retardation of the pulse-rate from stimulation there is an after-effect of a nature contrary to the immediate effect.

CHAPTER XVIII

Structure and Action of the Mammalian Heart

Dissection.—The human heart or that of a sheep should have been previously dissected to show its cavities and the blood-vessels connected with them, as well as the arrangement and action of the auriculo-ventricular and semilunar valves. The auriculo-ventricular bundle should also be shown.¹ A dissection may be made in a rabbit of the nerves accompanying the carotid artery (vagus, sympathetic, depressor).

Action of the heart in man.—Observe the chest wall over the situation of the heart: notice and feel the impulse or apex beat, strongest at one spot; mark this with ink. Apply the ear directly or through a binaural stethoscope over this spot, and also over the second right costo sternal articulation. Whilst listening to the sounds of the heart feel the carotid pulse of the subject, and determine that the first sound is systolic—*i.e.*, is synchronous with the rise of pressure in the artery due to the contraction of the ventricle; the second sound which immediately follows being diastolic.

Cardiographic tracing.—Apply the button of a cardiograph (Fig. 66) to the point where the impulse is most distinct, and take a tracing upon a moderately fast drum by the aid of a recording tambour.

An expiration should be made and the breath then held whilst the tracing is taken; this renders the apex beat more distinct and eliminates the movements caused by respiration. To obtain a good record a thin subject with a slow pulse should be selected, and he should be placed on a couch recumbent on his left side.

Rate of rhythm of the heart. Effect of position.—Count the rate of the heart beat by placing the finger either over the apex beat or upon an artery (pulse). Do this with the subject (1) recumbent, (2) sitting up, (3) standing up. Note down any differences you may observe in the rate and also in the character of the beat in these different postures.

Observation of the heart of a mammal *in situ*.—This observation may be made upon a “Sherrington” preparation.² The animal (cat)

¹ The mode of dissecting a sheep's heart is described in Pembrey's *Practical Physiology* and in Stewart's *Physiology*.

² See *Mammalian Physiology*, by C. S. Sherrington,

has been killed under chloroform anæsthesia by decapitation, the carotids having been first ligatured and the vertebrals occluded by a wire passed immediately in front of the axis vertebra, drawn tightly and securely fastened behind. Another ligature is made to include all the remaining structures of the neck except the trachea. The head is cut off by an incision in front of these ligatures, passing between the occiput and atlas. Oozing of blood is stopped by application of dilute adrenaline and plasticine; the skin is fastened over the cut end of the neck. Before tying the carotids, a tube has been inserted into

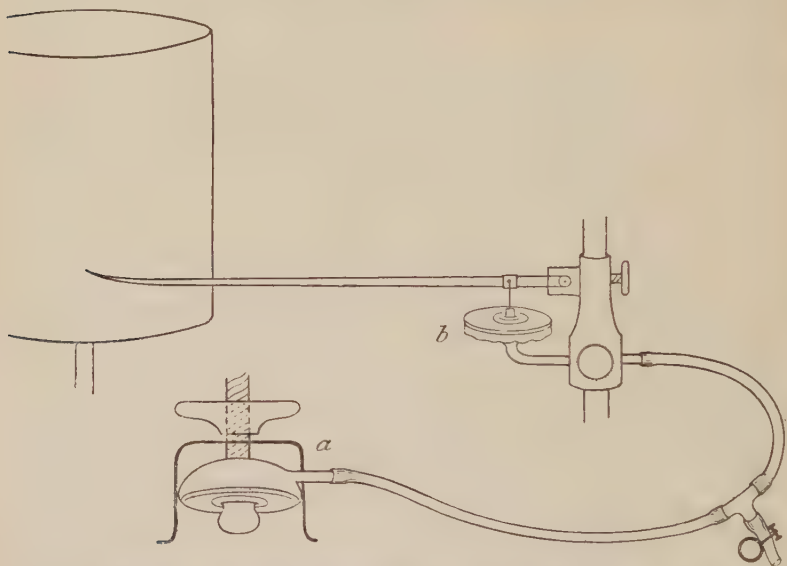


FIG. 66.—Diagram of Marey's cardiograph. *a*, receiving tambour for fixing over apex beat; *b*, recording tambour connected with *a* by rubber tubing, with a lateral opening closed by a clip.

the trachea, and artificial respiration is kept up by pumping air into the lungs and allowing it to escape by a side tube. This air is warmed. The body is further kept warm after decapitation by placing it on a warmed plate and covering it with cotton-wool. In such a preparation the circulation is maintained, although the pressure is somewhat low; the tissues continue to live for several hours. Spinal reflexes can be studied in it (see p. 124). The heart is exposed by severing four or five ribs or rib-cartilages on each side with bone-forceps (a ligature having first been tied round the upper end of the sternum so as to occlude the internal mammary arteries), and with the same

instrument the sternum is cut through near its lower end, and the detached part is forcibly raised, along with the cut ends of the ribs. It is not usually necessary to tie the severed intercostal arteries. The window thus opened discloses the heart within the pericardium; the latter may be cut open and the heart fully exposed. The systole, followed by diastole, of auricles and ventricles can be watched, and the hardening of the ventricles during their systole felt by applying the finger to their surface. By attaching one of the ventricles and one of the auricles by fine hooks and threads to light levers (Fig. 67), the

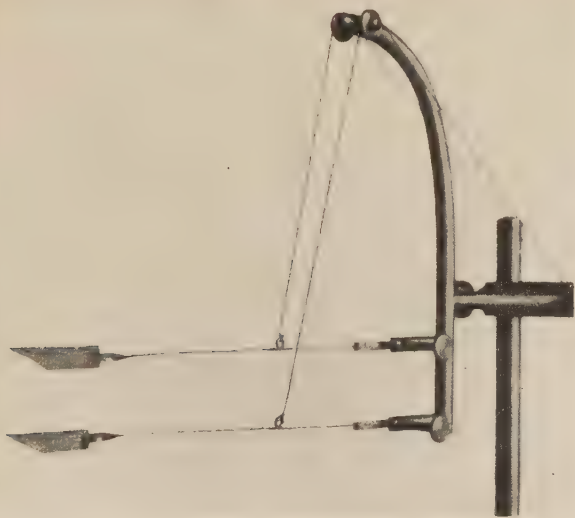


FIG. 67.—Cardiomyograph for obtaining simultaneous tracings from the auricle and ventricle of the exposed mammalian heart.

contraction of these parts can be recorded separately on a drum. The effect of stimulating the vagus in the neck and the action of atropine in abolishing this effect can be demonstrated; also the effect of stimulating the accelerator fibres which pass from the stellate ganglion of the sympathetic to the cardiac plexuses. The same result is obtained by stimulating the ganglion itself; this may be found by following the cervical sympathetic downwards. In the cat the vagus and sympathetic run in the same sheath in the neck, but they separate below and above. In the dog they are united in a common perineurium: in the rabbit they run separately from one

another, and a third nerve—the depressor—accompanies them in their passage down the neck.

The effect of adrenaline on the heart can also be shown in this preparation by injecting 1 c.c. of a solution of 1 in 10,000 into a vein ; or even by merely dropping some of the solution on the base of the exposed heart.

CHAPTER XIX

Methods of Investigating the Circulation in the Blood-Vessels

THE chief methods used can be practised upon a long india-rubber tube through which water is pumped from a reservoir by a rubber syringe actuated by an electro-motor. After passing through the system the fluid is again delivered through another rubber tube, controlled by a screw-clip, into the reservoir. A mercury kymograph (Fig. 68) and other manometers, such as Fick's C-spring (Fig. 69A), Fick's or Hürthle's straight-spring (Fig. 69B), as well as Ludwig's stromuhr (Fig. 70), and other instruments for measuring or estimating velocity, may be connected by means of T-tubes with the main india-rubber tube. The use of each instrument is to be studied separately, the others being temporarily shut off by screw-clips. Notice how the movement of any of the recording manometers may be damped by partially closing the tube connecting it with the main system. Observe the effect upon the pressure within the system (1) of increasing either the rate of the pump or the amount delivered at each stroke; (2) of diminishing or enlarging the outflow from the main tube by the screw-clip which controls it. This is equivalent to contraction or dilatation of the arterioles. Take a tracing with each form of manometer. Also record the amount of fluid passing through the stromuhr in one minute. Measure the diameter of the tubing in whose course the instrument is inserted, and calculate from these data the velocity of flow.

The velocity is found by dividing the amount flowing through the instrument in a second by the sectional area of the vessel ($V = \frac{v}{\pi r^2}$).

Plethysmography.—The arm of a subject (who is to be seated comfortably) is placed in a Mosso plethysmograph (Fig. 71), and this is allowed to rest on a table or in a sling. The junction with the arm is made by a broad rubber band. The interior of the plethysmograph is connected by rubber tubing with a recording tambour or piston-recorder; the whole is to be air-tight. The lever of the recorder registers respiratory and cardiac movements upon the smoked surface, since these movements produce changes in general arterial pressure,

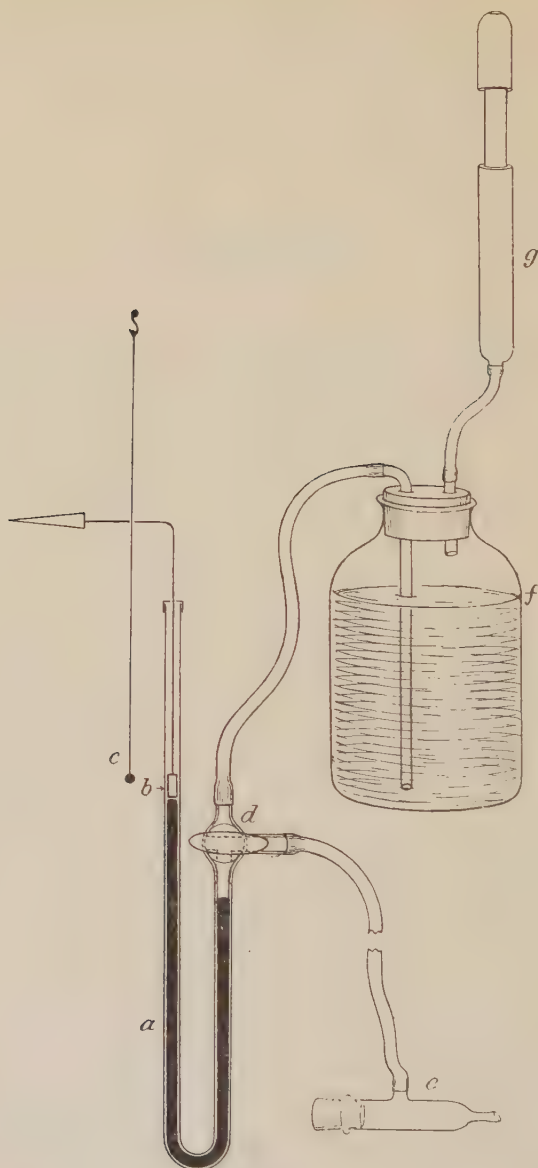


FIG. 68.—Diagram of mercury kymograph arranged for an experiment. *a*, bent glass tube containing mercury forming the manometer; *b*, aluminium float with rod, bent at right angles and ending in a writing point; *c*, small weight attached to silk thread suspended above writer and serving to keep it against the smoked paper; *d*, three-way stopcock; *e*, artery cannula; *f*, bottle of sodium carbonate solution; *g*, pump to raise the pressure: this may take the form of a rubber bag.

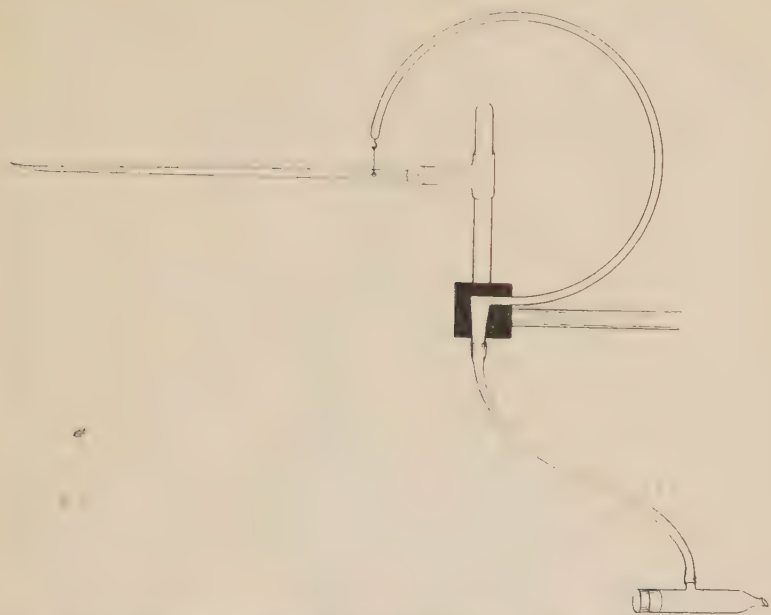


FIG. 69A. Diagram of Fick's C-spring manometer. Any increase of pressure within the hollow metal spring (which is filled with fluid) causes the C to open; any decrease of pressure causes it to close. These movements are communicated to the lever. The advantage of employing this or other spring manometer is that it has less inertia than the mercury kymograph. It must, however, be graduated by aid of a mercury manometer.

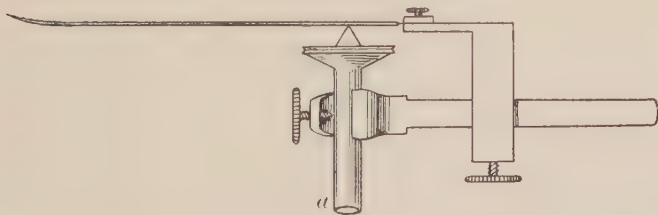


FIG. 69B.—Diagram to show the principle of Fick's or Hürthle's straight-spring manometer. *a*, tube terminating above in a tambour-like enlargement covered by a stout rubber membrane upon which is a metal disc and a wedge actuating a very light lever. The tube is connected by rubber pressure tubing with a cannula like that shown in Fig. 68, and the whole is filled with sodium bicarbonate solution.

and thus in the amount of blood driven into the arm. Compress the brachial vein above the elbow; the swelling of the arm due to retention of blood is at once shown.

Plethysmographs for the kidney, spleen, and other organs may be also studied (see Fig. 72). The principle of their action is the same as that used for the arm, but the form is adapted to each particular

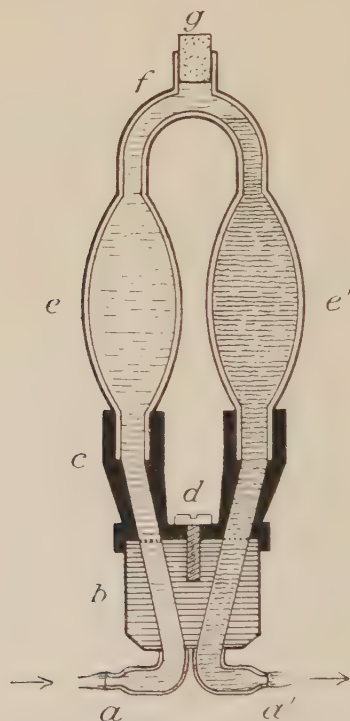


FIG. 70.—Ludwig's stromuhr. *a*, *a'*, cannulas for tying into cut artery; *b*, block on which the part *c* rotates around the axis, *d*; *e*, reservoir containing oil; *e'*, reservoir containing defibrinated blood; *f*, aperture for filling reservoirs, closed by cork, *g*.

organ. The glass cover as well as the gap (*g*) in the instrument through which the vessels and duct pass are made air-tight by vaseline.

In Mosso's original instrument, and in Roy's oncometer, which works on a similar principle, the apparatus was filled with fluid (water, oil); but this is unnecessary, air-transmission to a piston-recorder or tambour giving quite as accurate results, and being much more convenient.

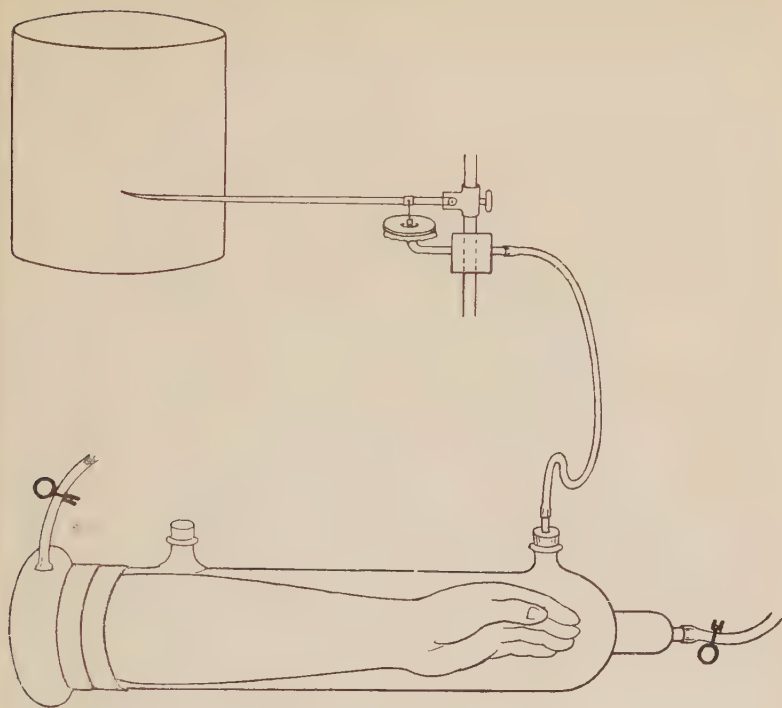
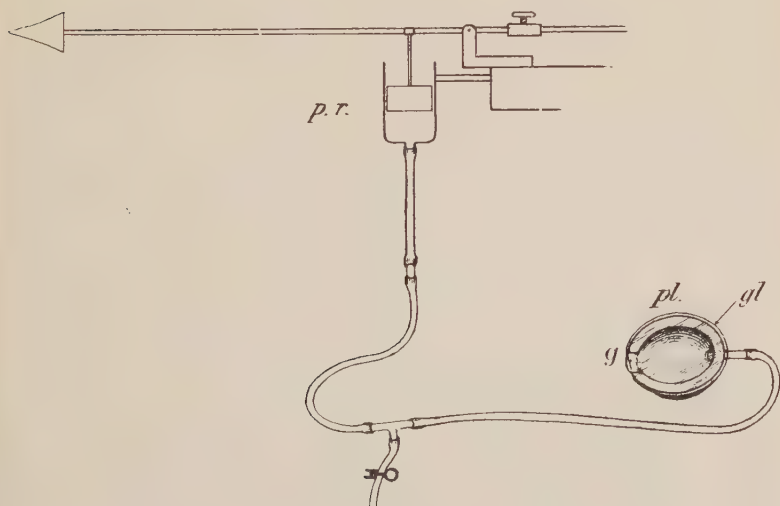


FIG. 71.—Mosso's arm-plethysmograph.

FIG. 72.—Diagram of organ plethysmograph. *pl.*, plethysmograph; *gl.*, glass cover; *g*, gap for passage of blood-vessels and ureter; *p.r.*, piston recorder.

CHAPTER XX

Study of the Circulation in Mammals

Study of blood-pressure, and the effects of nerves and drugs upon the heart and arteries in animals.—Either an anæsthetised animal, rabbit or cat, may be employed as the subject of a demonstration on blood-pressure, or a “Sherrington” preparation (p. 87) can be used by the student. A cannula (Fig. 68, *e*) is inserted into one of the carotids towards the thorax and tied securely in. If a dog is used the femoral artery may be employed instead of the carotid. The artery is previously ligatured beyond, and is clamped on the heart side of the place of insertion of the cannula. The cannula is connected, by a tube containing a half-saturated solution of sodium bicarbonate, with the proximal limb of a mercury manometer; a lateral tube affords communication with a reservoir of the same solution, which is under pressure. By this pressure the mercury is forced up in the distal limb of the manometer, so that the recording style is about 50 mm. above the abscissa or zero line. The clamp on the artery is then removed, and a record of the arterial pressure taken, a time-record (in minutes or fractions of a minute) being also inscribed. It is useful to record the respiratory movements at the same time (by tambours or otherwise). A blunt metal cannula, which fits the nozzle of a hypodermic syringe, is tied into one of the jugular or femoral veins towards the thorax: this is for the purpose of giving intravenous injections of drugs and extracts. A kidney, or the spleen, or a loop of intestine, or a limb, may be placed in a plethysmograph, and the changes of volume recorded. In the anæsthetised animal the following experiments may be made: for some of them the Sherrington preparation can be used:—

1. Effect of exciting the afferent fibres of a peripheral limb-nerve. Expose any limb nerve, tie a ligature tightly round the distal end of the part exposed. Stimulate the central end. Observe the effects on arterial pressure, on heart rate, and on respiration.
2. Put a drop or two of amyl nitrite on cotton-wool and allow the animal to inhale the vapour. Note the effect on blood-pressure.
3. Effect of exciting the vagus. One of the vagi in the neck having

been isolated for a short distance, taking care to avoid injuring it, a thread is tied tightly round it: this serves to hold it, and also severs the continuity of its fibres, and is therefore equivalent to cutting it across. (a) Stimulate the end below the ligature. Observe the effect on blood-pressure caused by cardiac inhibition. (b) Stimulate the upper end. Observe the reflex effects on blood-pressure and on respiration which are produced. (c) Stimulate the superior laryngeal branch, which can be seen passing to the larynx. Observe the effect on respiration and blood-pressure.

4. Effect of cutting both vagi. The ligature of the one vagus—which, as just explained, severs its fibres—produces little or no effect on blood-pressure or respiration. Now tie or cut the other vagus also. Notice the effect, if any, (a) on respiration, (b) on blood-pressure. Repeat the excitation experiments.

5. Inject solution of atropine sulphate (about 2 milligrammes) into the jugular vein. Notice the effect, if any, upon blood-pressure and respiration. Repeat the excitation of lower and upper ends of vagus as in (1), and note results.

6. If a rabbit is used, two other very fine nerves can be found in the neck accompanying the carotid artery and vagus. One of these is the depressor: it is a branch of the vagus or of the superior laryngeal or of both. The other is the cervical sympathetic: it passes above into the superior ganglion. Both these nerves are to be tied low down. After tying the sympathetic, the pupil of the eye on that side will be more contracted than the other, the third eyelid will be partly drawn over the globe, and the ear of

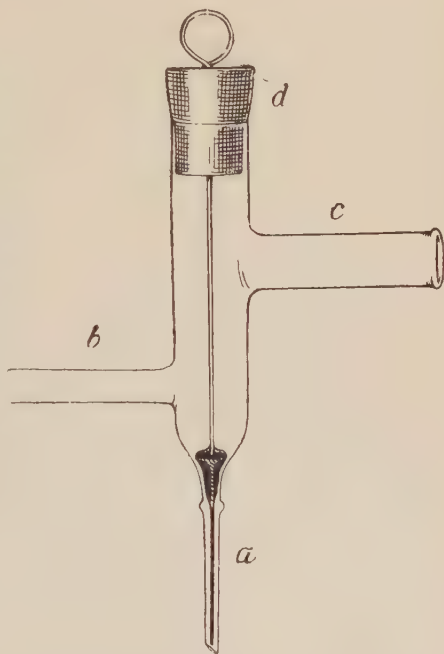


FIG. 73. —Cannula for insertion in the pulmonary artery through the wall of the right ventricle. (a) open end of cannula with plug of Chatterton's cement attached to wire passing through cork, d; b, lateral tube for connecting with recording apparatus; c, wash-out tube.

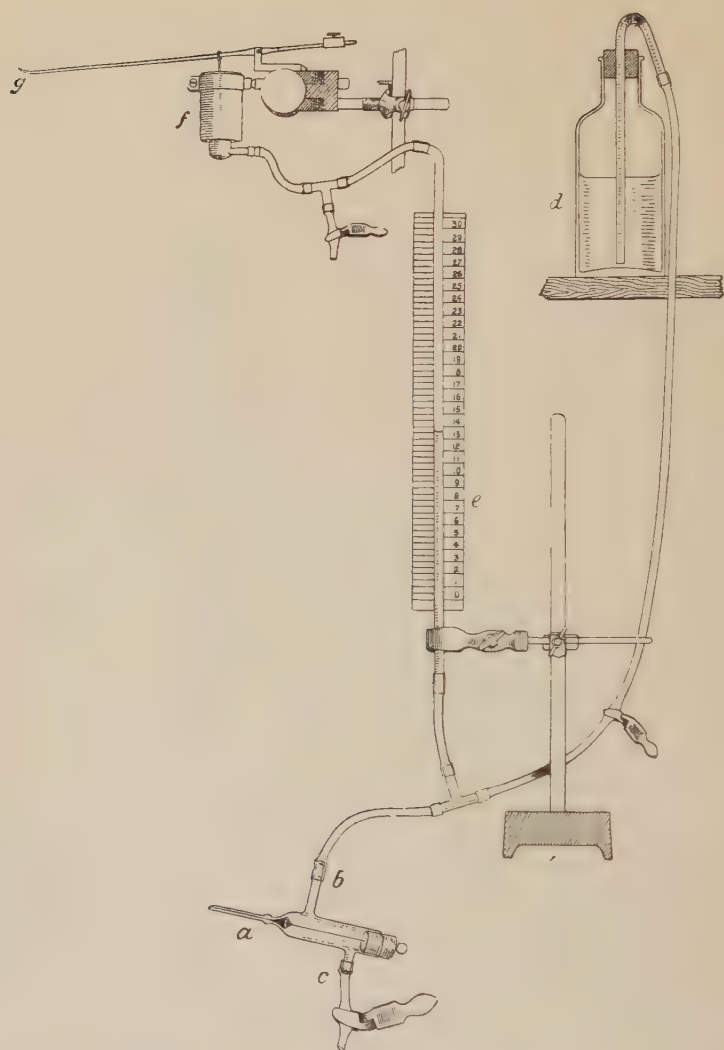


FIG. 74.—Diagram of method of recording the blood-pressure in the pulmonary system. *a*, *b*, *c*, as in Fig. 73; *d*, bottle of bicarbonate solution with loosely fitted cork; *c*, manometer tube with scale in centimetres and millimetres; *f*, piston-recorder; *g*, writing point,

that side will be warmer and redder. (a) Stimulate the upper end of the sympathetic: the pupil dilates, the third eyelid is retracted, some of the hairs on the side of the head may be erected, and the arteries of the ear contract, so that the whole ear becomes pale. (b) Stimulate the upper end of the depressor whilst the blood-pressure is being recorded. After a period of latency there is a fall of pressure which lasts during stimulation of the nerve and for a short time after its cessation. (c) Expose the stellate ganglion in the uppermost part of the thorax, after resecting the first rib (before this can be done artificial respiration must be set going). Stimulate the ganglion and observe the effects on the pulse and blood-pressure.

7. Inject into the jugular vein a few drops of an extract of the suprarenal capsule of any animal, or a small dose of adrenaline (1 c.c. of 1 part in 20,000). The extract is made by taking 20 c.c. of Ringer's solution to each gramme of suprarenal capsule, boiling and filtering. Record the effect on blood-pressure. Notice the dilatation of the pupils, the retraction of the third eyelid, and the pallor of the ears. If a plethysmograph is being used, the record of the effect on the contained organ usually indicates contraction of arteries. The experiment can be repeated more than once.

8. Inject into the jugular vein a few drops of an extract of ox-pituitary. The extract is made in the same way as the suprarenal extract. The posterior lobe only should be used. Notice the effect of the extract upon the blood-pressure and upon the plethysmograph record. If the injection is repeated after a short interval, most of the results are not shown, or are much less marked.

9. Kill the animal by asphyxia—which may be effected by occluding the trachea or by allowing carbon monoxide gas (or coal gas) to be respired. A continuous tracing showing the effects of asphyxia, both upon the respiratory movements and upon the blood-pressure and heart beats, may be recorded.

The pulmonary circulation.—The blood-pressure in the pulmonary artery may most easily be obtained by the use of a specially constructed cannula which is passed into the commencement of the artery, through the ventral wall of the right ventricle. The cannula, filled with half-saturated bicarbonate of soda solution, is tied in the wall of the ventricle by a purse-string suture and is furnished with a plug, to prevent escape of blood while it is being inserted. Its construction will be understood from Fig. 73. It is connected with a vertical glass tube, with scale attached (Fig. 74), which serves as a manometer, giving the pulmonary pressure in centimetres and millimetres of the solution. The pressure is recorded upon the blackened paper of the kymograph, by a piston-recorder connected with the open end of this manometer, and is

written down simultaneously with the pressure in the systemic arteries recorded by the mercurial manometer.

As the thorax has to be opened to expose the heart and insert the pulmonary cannula, artificial respiration must be maintained throughout the operation (p. 88); but it is possible to sew up the thorax (with the lungs distended) and to continue the experiment with natural respirations.¹

¹ For a more complete description of this method of studying the pulmonary blood-pressure, see the *Quarterly Journal of Experimental Physiology*, vol. xii., p. 133.

CHAPTER XXI

The Capillary Circulation

THE flow of blood in the smallest arteries and veins and in the capillaries is observed with the microscope in transparent parts of animals, such as the web and mesentery of the frog, the tail of the tadpole, the lung and tongue of the toad, and the mesentery of small mammals.

1. **In the frog's web.**—The frog, the brain of which may be destroyed, is immobilised with curari or by immersion in water saturated with chloroform or ether. The animal is laid on a flat cork with

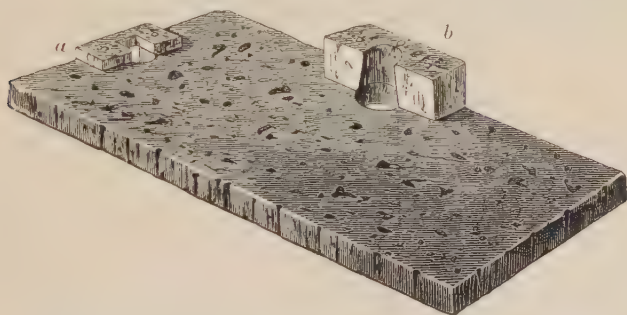


FIG. 75.—Frog-cork for displaying mesentery, lung, tongue, or web of foot.

a slot at one end (Fig. 75, *a*): the margins of this are raised in the way shown in the figure, and the web of one foot is spread out over the slot with the aid of pins and threads, but not stretched so tightly as to obstruct the circulation. If a low power of the microscope is used the web need not be covered with a cover-glass.

2. **In the frog's mesentery.**—For this a hole is made at one side of the cork (Fig. 75, *b*) with its margins raised somewhat higher than for the web. The hole is covered by a circular disc of glass, not too thick, fixed to the cork with sealing wax. A loop of intestine is drawn out through an aperture in the abdominal wall, and arranged round the

glass disc in the manner shown in Fig. 76, with the mesentery resting on the disc. The mesentery must be kept wet with Ringer's solution; it may be covered by a very thin cover-glass. A high power can then be used.

3. **In the tadpole's tail.**—To observe the flow of blood in this structure all that is necessary is to immobilise a tadpole with water shaken up with ether, and place it upon a glass slide in the same fluid. The thin edges of the tail are observed with the microscope.

4. **In the toad's lung.**—This is prepared much in the same way as the frog's mesentery. The lung is allowed to protrude from an aper-

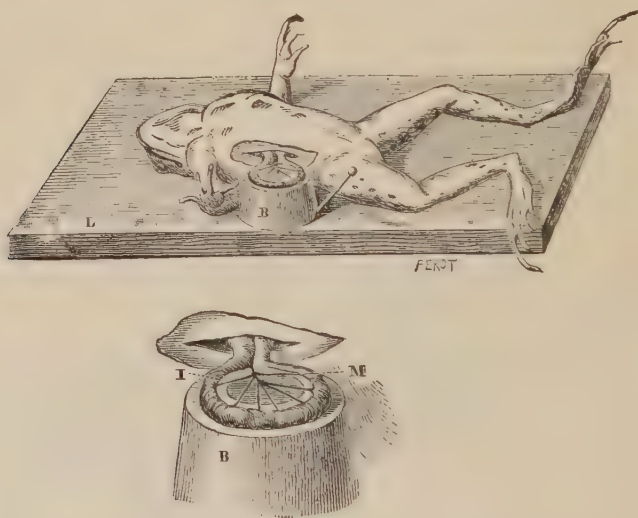


FIG. 76.—Method of displaying frog's mesentery for microscopic observation (Ranvier). L, glass or cork plate; B, cork, with cylindrical hole through it; I, intestine; M, mesentery.

ture in the side of the thorax and to rest on the mesentery disc. The toad is used in preference to the frog because its lung normally remains distended with air, and requires no special appliance for keeping it filled.

5. **In the toad's tongue.**—This is on the whole the best object for the study of the capillary circulation in cold-blooded animals: the frog's tongue is not quite as good.

The animal is immobilised as before, and is laid on the frog-cork on its back, with the end of the snout near the slot *a*. The lower jaw is then raised, and the tongue, which is naturally folded back in the mouth,

is drawn forward, and is fastened, with as little injury as possible, by fine pins over the slot. There is a large lymph sac in the organ: this is to be distended by Ringer's solution with the aid of a hypodermic syringe. The mucous membrane which is now uppermost is of some thickness; it is slit up longitudinally with fine scissors, and pinned to either side, any escaped blood being got rid of by rinsing with Ringer. The delicate internal structures of the tongue are thereby exposed (muscle-fibres, connective tissue, and blood-vessels), and can be examined in detail with a high power of the microscope after covering with a light cover-glass.

6. **In the mesentery of small mammals such as rats and mice.**—The method is generally similar to that used for the frog-mesentery, but anæsthetisation must be produced by drugs such as urethane or chloral hydrate administered either enterically or hypodermically, and special measures are necessary to keep the exposed mesentery warm and moist whilst under observation.

7. **In the human skin.**—By using a powerful illumination it is possible, with the aid of a good stereoscopic microscope, to observe the circulation in the capillary vessels of the skin of certain parts, *e.g.*, at the base of the finger nail.

Capillary Pressure

The pressure of the blood in the capillaries is studied (1) by the method of Roy and Graham Brown, and (2) in man by the method of v. Kries.

1. The web of the frog or the mesentery of any small animal is observed by a low power of the microscope through a fixed plate of glass, with the lower surface of which it is brought in contact. Pressing against the under surface of the preparation is a small bag of gold-beater's skin filled with water and connected with a reservoir of the same fluid. By raising or lowering the reservoir the pressure on the preparation can be varied: it is measured by a manometer. The capillary pressure is taken as equivalent to that which just permits the circulation in the preparation to be maintained.

2. A small glass plate of known area and weight is allowed to rest on the skin at the root of the nail of one of the fingers, the hand being held in a horizontal position at about the level of the heart. Weights are placed upon the plate until the skin below is blanched by the pressure. This pressure is expressed as water-pressure by a calculation based on the fact that a gramme represents the weight of 1,000 cubic

mm. H_2O . Thus, supposing the area of the glass plate to be 20 sq. mm. and that the skin below it is blanched by a weight of 5 grammes (including the weight of the glass plate), each sq. mm. would be subject to pressure equal to that of a column of water of $\frac{5.000}{20}$ mm. in height, *i.e.*, 250 mm. But capillary pressure is subject to so much variation from the result of gravity, local conditions of the tissues, etc., that its determination can at best be only approximate.

CHAPTER XXII

The Pulse. Arterial Pressure in Man

The pulse in the arteries.—Feel the pulse in the radial artery and determine and note (1) its rate and regularity, (2) its quality, whether hard or soft, bounding, readily compressible, etc. Apply a *sphyg-*

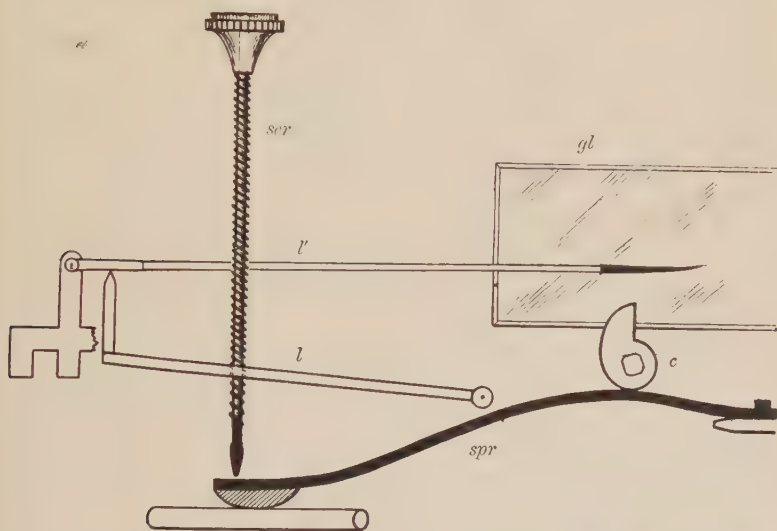


FIG. 77.—Diagram of Marey's sphygmograph. *spr*, spring with button for resting on radial artery; *c*, cam, for exerting pressure on the spring; *scr*, screw connecting spring with double lever *l*, *l'*; *gl*, smoked glass or paper for writing the pulse.

mograph, either Marey's original pattern (Fig. 77) or the modification devised by Dudgeon (Fig. 78). Using the cam, exert such pressure upon the spring of the sphygmograph as will allow the variations in pressure within the artery to be most manifest. The tracings are taken on slips of paper smoked over a candle. Write on each slip the name of the subject of the experiment and the pressure which was employed; varnish and preserve.

Effect of muscular exertion.—Determine the effect upon the pulse-rate of different positions of the body, viz.: lying down, sitting, standing; and also the effect of muscular exertion, such as lifting heavy weights or ascending stairs. Find out how soon after such exercise the pulse-rate returns to normal.

The venous pulse.—In a recumbent subject hold a small receiving tambour without rubber membrane (a small thistle funnel will do) over the place in the lower part of the neck where the venous pulse

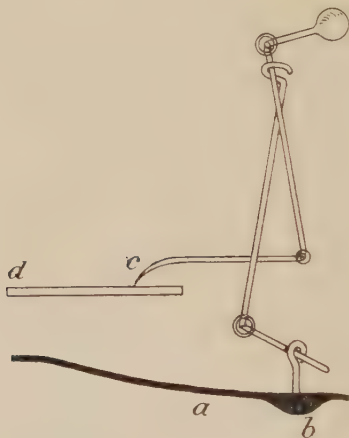


FIG. 78.—Diagram to show the lever-mechanism of the Dudgeon sphygmograph. *a*, spring; *b*, button to be applied to the radial artery; *c*, writing point of jointed lever attached to spring; *d*, glass plate or paper on which the tracing is recorded.

in the jugular is most distinct. This receiving tambour, the edges of which can be made airtight by vaseline, is connected by rubber tubing to a recording tambour, and the curve is written on paper moved slowly by clockwork. A tracing of the carotid pulse can be obtained on the same paper, another tambour provided with a rubber cover and a button being fixed over the artery. A convenient apparatus for taking such tracings is the *polygraph* of Mackenzie. In this instrument there is a continuous roll of white paper on which the tracings are recorded with ink.

Arterial pressure in man.—The pressure of the blood within the human arteries is determined by the *sphygmometer*, of which many forms are in use. All have a circular rubber bag (Fig. 79, *a*) which is enclosed by leather and is placed round the upper arm. The bag is distended with air by a pump (*c*), the amount of pressure used being

recorded either by a mercury manometer (Riva-Rocci) (*b*) or an aneroid (Hill and Barnard) or by compression of air in a closed tube, using a coloured fluid (Hill) or mercury as index (Oliver). As the distension

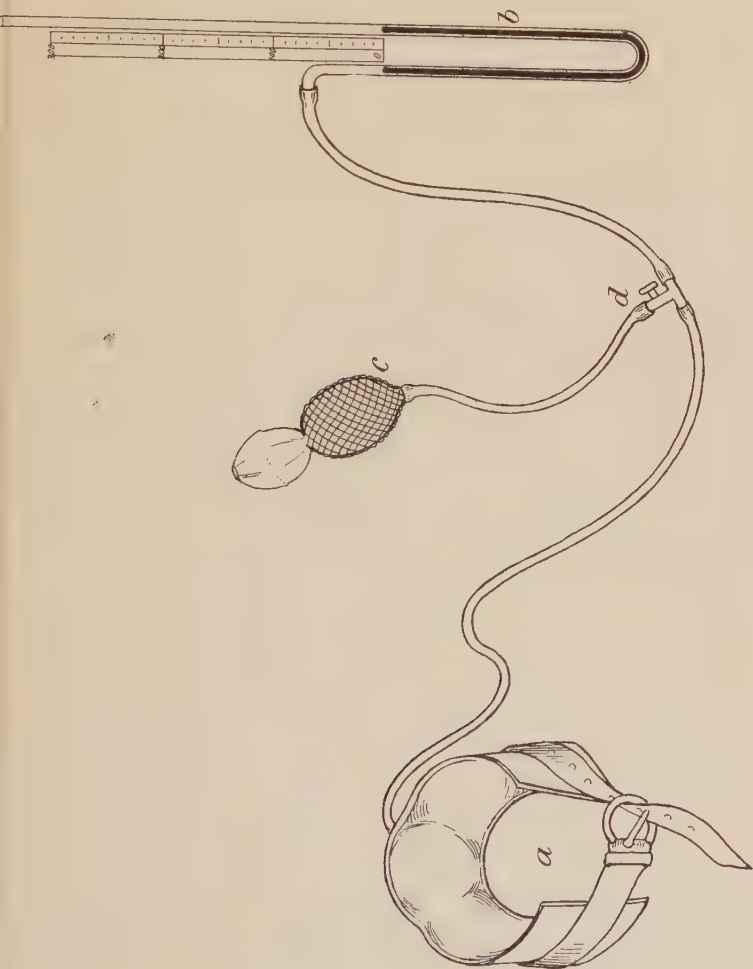


FIG. 79. — Riva-Rocci apparatus for determining arterial pressure in man. *a*, leather arm-band with rubber bag as lining; *c*, pump for forcing air into the bag; *d*, valve for letting air out of the system; *b*, mercury manometer.

progresses the manometer shows not only the gradual increase of pressure, but also oscillations due to the pulse. These oscillations increase in magnitude up to a certain point. The lower reading when the oscillations are greatest is the measure of *diastolic pressure*, as the artery will expand maximally when the pressure outside is just equal to the arterial pressure during diastole. The point around which

the oscillations are greatest is the measure of *average pressure*. On further raising the pressure the oscillations again become smaller, as the brachial artery is now becoming occluded. When it is completely occluded the pulse ceases to be felt at the wrist; this point is the measure of *systolic* or *maximal pressure*. It should be confirmed by very gradually diminishing the pressure and noting the point at which the radial pulse reappears.

It is not always easy to determine the exact point at which the pulse ceases to be felt. The difficulty is lessened by attaching a small tambour connected with a binaural stethoscope over the brachial artery at the elbow. As the pressure is raised over the upper arm the pulse beats become heard as distinct taps in the artery at the elbow, but when the pressure is sufficient to occlude the brachial the taps cease. On letting out air and thus diminishing pressure in the armlet the taps reappear. The point at which they again become distinct indicates the systolic pressure in the artery, and corresponds with that at which the pulse just reappears in the radial.

The interpolation between the pump and the manometer of a bag which can be squeezed or allowed to relax by a simple screw adjustment in the manner recommended by Oliver, enables the observation to be repeated at will, without the necessity of again pumping air in or letting air out of the apparatus.

CHAPTER XXIII

Perfusion of Vessels. Lymph-Hearts

Estimation of contraction or dilatation of vessels by measurement of perfusion rate.—Tie a small glass cannula, bent round so that its limbs are parallel, into the aorta of a large frog killed by destruction of the nervous system; the cannula can either be passed directly into the cut aorta or more easily through an incision in the ventricle. In exposing the heart and aorta make as small an opening as possible. First remove a flap of skin, then cut through the upper part of the ensiform cartilage, and extend the incision on either side of the sternum: force this up like a flap until the heart is sufficiently exposed.

The cannula must be filled with Ringer's solution, and connected through an india-rubber tube with a reservoir of the same fluid, which is allowed to drop slowly from it during the introduction; this is for the sake of excluding air bubbles.

Suspend the frog by a pin through the jaw, and fix the reservoir a short distance above the head so that the fluid flows into the vessels by gravitation. Make a cut into the sinus venosus to enable the fluid to flow freely out after it has traversed the blood-vessels of the body; the escaping fluid will drip from the toes, which should be tied together. A cut must be made through the skin of each foot to prevent accumulation in the lymph-spaces of the legs. Count the number of drops per minute, and repeat the counting twice: after the blood is completely washed out the flow should be fairly regular.

To test the effect of drugs or reagents upon the muscular tissue of the arterioles the reagent is added in known quantity to the perfusing fluid. The Ringer's solution to which the drug is to be added is placed in a second reservoir, as in perfusion of the frog-heart (see Fig. 63, p. 80). Again count the number of drops per minute (three estimations), and thus determine whether the arterioles are becoming dilated or contracted as the effect of the reagent. This experiment may be tried with Ringer's solution containing acid (HCl, 1 in 5,000) and alkali (NaOH, 1 in 5,000), with a very dilute extract of suprarenal, with barium chloride, and with solutions of chloroform and ether in Ringer's solution. Normal Ringer's solution must invariably be substituted

afterwards for that containing the drug, and a third determination made in the same way (average of three counts).

The same method is used for perfusion of the organs of mammals. The cannula is tied into the artery of the (excised) organ, which is placed in a jacketed funnel warmed to 38°C .: the perfused fluid, which must also be warmed before entering the organ, escapes by the vein and runs down the funnel into a measuring vessel. In this way perfusion can be conducted through the kidney of the dog or sheep, or

through the vessels of a limb. In mammals it is usual to allow oxygen to bubble through the Ringer solution used for perfusion and to add gum arabic to the Ringer to prevent œdema (Bayliss). It is also advantageous to render the pressure variable by intermittently checking the inflow, thus imitating the arterial pulse.

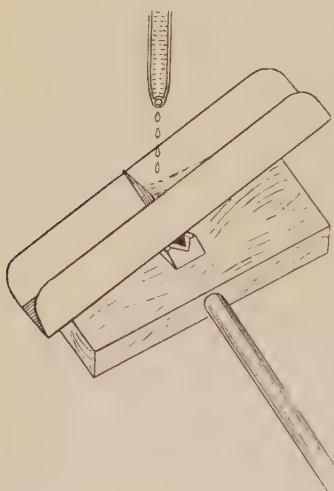


FIG. 80.—Diagram of tilter. The rocking movements are recorded either by allowing the accumulated fluid to actuate a tambour, or by an electro-magnetic signal.

Methods of recording the outflow of fluid.—1. The sequence of drops of any fluid can be recorded by aid of an electric drop recorder connected with an electro-magnetic signal, which writes upon the smoked paper of a drum.

2. Another method of graphically registering the rate of flow, especially if the drops follow one another too fast to be recorded individually by a drop-recorder, is furnished by the “tilter” shown diagrammatically in Fig. 80. This is a small vulcanite or celluloid trough with open ends, with a septum across the middle; the trough is balanced on a vulcanite knife-edge. The drops are led over the middle, and, falling on the side of the septum which happens to be uppermost, they gradually fill that side of the trough. When full, it overbalances, and the trough tilts over to the other side, when the process is repeated. Each movement of the tilter is registered, either by an electrical or a pneumatic arrangement, upon the recording paper, on which the time is also written. The capacity of the tilter being known, the amount of fluid flowing in a given time is ascertained. The record will continue automatically for long periods.

3. A third method is to allow the fluid to flow into a vessel of

known capacity which intermittingly and automatically empties itself by a siphon: each emptying being recorded graphically on the moving smoked paper.

The above methods may also be used to record the flow of secretions (Chapter XXIV.).

Lymph-hearts.—Fix a frog, the brain of which has been destroyed, or which has been decapitated, in the prone position on the frog-cork, and reflect the skin from either side of the urostyle. Notice the pulsation of the lymph-hearts beneath the fascia on each side: usually they do not synchronise. Destroy the spinal cord completely by a wire. The lymph-hearts now cease to beat: their pulsations are dependent on the spinal cord.

CHAPTER XXIV

Mechanism of Secretion

THE process of secretion may be studied in the salivary glands, the pancreas, the kidneys, and the mamma. The influence of nerves upon secretion is illustrated by the salivary glands, that of autacoids by the pancreas and mamma. The secretion of the kidneys is also dependent partly upon chemical agents, but largely upon the blood-pressure and blood-flow through the organ. The following experiments are suitable for demonstration.

The submaxillary gland.—A dog, having been anæsthetised, is fixed on its back and a vein-cannula inserted into a saphenous vein. An incision is then made on one side through the skin and fascia below the mouth, extending from the chin backwards for 3 or 4 inches nearly parallel with the line of the lower jaw. At the posterior part of the wound the submaxillary gland may be observed. The anterior belly of the digastric, which comes into view and conceals the hilum of the gland, is drawn over laterally by a weighted hook: or it may be cut away. Any oozing from small vessels is controlled by rinsing the wound with dilute extract of suprarenal; larger vessels are tied. A muscle—the geniohyoid—is now exposed: it is composed of transverse fibres. When it is cautiously cut through, the duct of the submaxillary gland (Wharton's duct) is seen passing obliquely forwards towards the floor of the mouth. It is accompanied by a smaller duct, that of the sublingual. Crossing these ducts is a conspicuous nerve—the lingual branch of the 5th. If this is drawn towards the middle line with a blunt hook, it is seen that just before it crosses the ducts it gives off a small nerve—the chorda tympani—which curves sharply backwards and enters the hilum of the submaxillary gland, whence the duct is emerging. Tie a thread around the lingual above the place where the chorda leaves it, and, without injuring it, clear a short length of the chorda so that a small pair of flat electrodes can be placed underneath it. Stimulate by induction shocks: the duct will fill with saliva.

Place a wet thread round the duct and slip a pointed piece of paraffined paper under it. Make a snip into it with fine scissors;

pass a "finder" into the aperture. Substitute for the "finder" a very fine metal or glass cannula, and tie this in: a piece of small rubber tubing can be used to conduct the secretion beyond the edge of the jaw, where it may be allowed to drop into a beaker.

On the same side of the neck make a longitudinal incision through the skin and fascia, and separate the muscles so as to expose the carotid artery and the common trunk of the vagus and sympathetic nerves. Ligature this combined nerve low down, and place the upper end on a second pair of electrodes. The two pairs of electrodes—for chorda and sympathetic respectively—are connected to a commutator without cross-wires, and this with the secondary coil, so that stimulation can be led into either pair at will.

1. Stimulate the sympathetic. A few drops of thick viscid saliva are secreted. (In the cat, stimulation of the sympathetic yields an abundant secretion.)

2. Stimulate the chorda. There is a rapid flow of watery saliva, lasting as long as the excitation is continued.

3. Inject a small amount of pilocarpine nitrate (2 or 3 milligrammes) into the saphenous vein. This produces an intense secretion.

4. Inject a small amount of atropine sulphate (5 milligrammes) into the vein. The flow produced by pilocarpine immediately stops.

5. Stimulate the chorda. The strongest stimulation produces no effect. Atropine has paralysed the nerve endings.

6. Stimulate the sympathetic. Saliva will be secreted as before. The dose of atropine is insufficient to abolish the action produced through the sympathetic.

The pancreas.—A dog is anaesthetised and a cannula tied into the saphenous vein. Open the abdomen by an incision in the linea alba. Find the duodenum and bring it to the surface: the pancreas is seen in the mesentery within its curve. The main duct of the gland—canal of Wirsung—may be found without difficulty near the lower end of the part of the gland which is in contact with the duodenum. Isolate a short length of the duct with forceps; pass a wet ligature round it and slip a pointed piece of paraffined paper under it. Make a snip into the duct with fine scissors, introduce a finder, substitute for the finder a fine metal or glass cannula, and tie this in. Attach a short piece of rubber tubing to the cannula, bring the end of this outside the wound, and let the drops of secretion fall into a beaker.

1. Inject into the saphenous vein 5 c.c. of an extract of duodenal mucous membrane of any animal. The extract is made by boiling the chopped mucous membrane with 0.5 per cent. hydrochloric acid, cooling the decoction, neutralising with dilute alkali, and filtering. It con-

tains an autacoid (*secretin*), which has the effect of producing a rapid flow of pancreatic juice when injected into the circulation.

2. Inject pilocarpine nitrate and compare the effect with that of secretin.

The mamma.—A lactating animal (cat) is anæsthetised and a cannula tied into the external jugular vein. Vaseline the fur over one of the mammæ, and arrange the animal so that this gland slightly overhangs the edge of the animal board. Cut away the nipple of that mamma and make an incision into the gland through the base of the nipple. Still any bleeding with cotton-wool or with dilute suprarenal extract. Some milk may ooze out: it will run down the vaselined fur, and can be caught in a beaker.

1. Inject into the vein 1 c.c. of a 10 per cent. decoction of corpus luteum (filtered). Milk will exude and drop rapidly from the gland.

2. Inject into the vein 1 c.c. of a 10 per cent. decoction of posterior lobe of pituitary body. The same result will ensue, but the flow will be more rapid.

The kidney.—In an anæsthetised rabbit or cat tie a cannula into the jugular vein and connect the carotid with a manometer for registering blood-pressure. Make an incision through the skin and muscles on the left side of the abdomen near the back over the situation of the kidney, which is easily felt. After exposing the kidney, bring it towards the surface, partly clear it of fat, and allow it to lie in a suitable plethysmograph (Fig. 72), the margins of which have been vaselined, and place over it a glass cover also well vaselined: the cover is clipped down on to the plethysmograph. The blood-vessels and ureter pass out at the chink (*g*) left on one side of the plethysmograph: the chink is made airtight with vaseline. A tube leads from the plethysmograph to a piston recorder (*p.r.*) writing on smoked paper. Make another incision in the lower part of the abdomen in the middle line; find the urinary bladder; hold it up with two pairs of clamp forceps; loop a ligature round it just beyond these; make an incision into it, and introduce a glass cannula, which must then be tied in. The urine is led from this cannula over the side of the animal by a rubber tube, the end of which must be below the level of the bladder so that this organ is constantly drained. The drops can be registered by a drop-recorder (*p.* 110).

1. Inject 20 c.c. of Locke's solution slowly into the vein. Record the effect on blood-pressure, on kidney-volume, and on amount of urine secreted.

2. Repeat this experiment, using the same amount of Locke's solution, but with the addition of half a gramme of urea.

3. Inject 1 c.c. pituitary extract into the vein, and, as before, record the effect on blood-pressure, kidney-volume, and urine.
4. Inject 5 c.c. of Locke's solution containing 5 milligrammes of caffeine citrate, and record its effect in the same way.
5. Inject atropine sulphate (5 milligrammes) similarly. This has no effect on the secretion of the kidney (compare its effect on salivary secretion).

CHAPTER XXV

Respiration

The respiratory movements in man.—Examine the bared chest during quiet respiration, and notice the parts in which movement is most evident; the same with forced respiration. Observe the alteration in

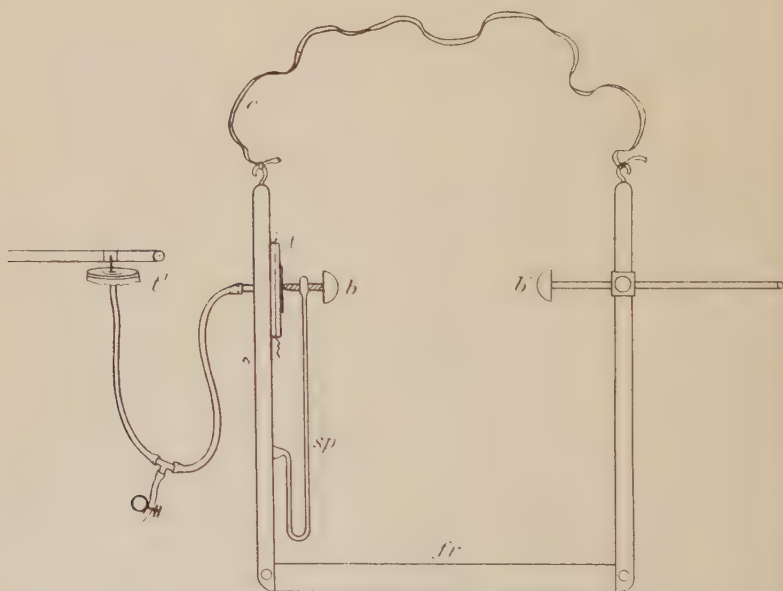


FIG. 81.—Sanderson's stethograph. *fr*, frame suspended over the shoulder by cord, *c*; *b*, *b'*, buttons applied to opposite sides of the chest wall; *sp*, steel spring; *t*, receiving tambour; *t'*, recording tambour.

obliquity and other changes in position of the ribs, rib-cartilages, sternum, and epigastrium. Apply the ear directly or through a stethoscope to the chest wall and listen to the vesicular murmur; listen also over the larger bronchi and trachea. Count the rate of respiration and compare it with that of the pulse of the same individual.

For the following experiments the slowest rate of drum is to be used, and the subject must not be allowed to see the tracing which is being taken.

Record of respiratory movements.—Apply a stethograph (Marey's or Sanderson's) (Fig. 81) to the chest, and register the movements of respiration by means of a recording tambour.

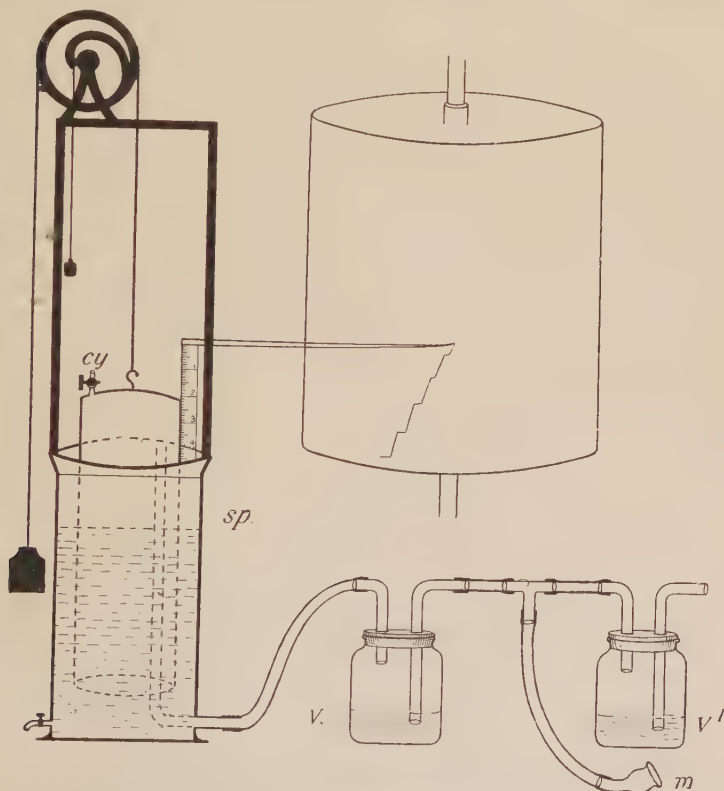


FIG. 82.—Spirometer arranged to register, upon a slowly revolving drum, the amount of air respired. *sp.*, body of spirometer; *cy*, measuring cylinder with scale and writer attached; *v*, *v'*, water valves; *m*, mouthpiece.

Remove the lever of the recording tambour from contact with the drum. Cause the subject to take a number of deep respirations at a rapid rate. Then let him cease these voluntary efforts; take a record of the breathing which succeeds them. There will probably be a pause (apnœa), followed by respirations which are at first shallow but gradually become of the ordinary character.

Next, let the subject abstain from breathing (after an ordinary expiration) for the space of half a minute, and record the respiratory movements which succeed the abstention (dyspnœa).

Lastly, allow the subject to respire a mixture of air and CO_2 (10 per cent.) contained in an oil-silk bag or a gasometer, and again record the movements of the chest wall.

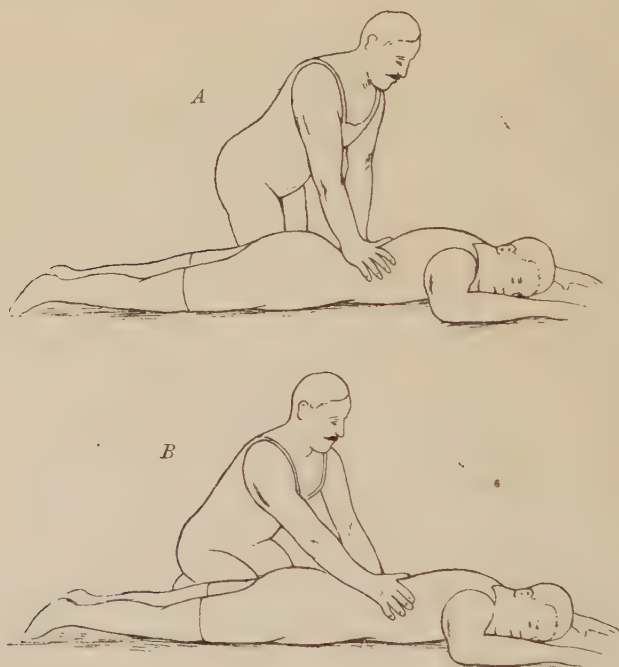


FIG. 83.—Prone-pressure method of artificial respiration. *A*, pressure being applied; *B*, pressure removed.

Measurement of tidal air passing into and out of lungs.—Using either an airtight mask or a mouth-tube provided with valves (in this case the nostrils must be closed by a clip) allow the subject to breathe during one minute into a carefully balanced spirometer (see diagram, Fig. 82). Count the number of respirations in a given time, and note the amount of air which has been breathed in that time. From these results calculate the tidal air passing through the lungs with each respiration. The observation should not be begun until the subject is breathing regularly and unconsciously, and he must not be permitted to see the movements of the spirometer.

Reserve air, supplemental air, vital capacity.—Determine in your own person with the spirometer the amounts of each of these, and note down the results.

Measurements of the chest and abdomen in deepest inspiration and in deepest expiration.—Determine these upon yourself (*a*) at the level of the armpits, (*b*) at the level of the lower end of the sternum, (*c*) at the level of the umbilicus, using a tape measure. Note down the results.

Artificial respiration in man.—Place the subject flat on the ground in the prone position with the head on one side. Kneel or squat by the side of or across the lower part of the body, facing the head, and place your hands flat on the loins with the thumbs nearly touching at the spine (Fig. 83). Throw the weight of your body forward on the hands, keeping your arms straight (*A*), and count slowly *one, two, three, four, five*. Whilst counting *four, five*, swing backwards (*B*) so as to take the weight off your hands. Then swing forwards again, counting, as before, *one, two, three*; and backwards, counting *four, five*; and so on twelve to fifteen times a minute. The effect of the pressure is to force the abdomen and lower part of the chest against the ground so that the viscera are pressed against the diaphragm. In this way air is driven out of the lungs. On relaxing the pressure the parts resume their former position; the diaphragm descends and air is drawn into the lungs.

The amount of air thus pumped through the lungs in a minute may be measured by the spirometer in the same way as the tidal air measured in natural respiration.

Negative pressure within thorax.—Introduce through an intercostal space into the pleural cavity in the human cadaver or in any dead animal a sharp-pointed cannula or hollow trochar connected by rubber tubing to a water manometer. Notice that as soon as the trochar communicates with the pleural space the water in the distal part of the manometer sinks and registers a certain amount of negative pressure within the thorax (Donders' experiment).

Effects of stimulation of nerves and of asphyxia upon the respiratory movements of animals.—These have been studied in connexion with blood-pressure (Chapter XX.).

CHAPTER XXVI

Nerve-Roots

Nerve-roots.—Decapitate a large frog and fix it securely in a prone position on the frog-cork. Cut away the skin along the whole length of the spine. With a pair of strong but fine scissors sever the neural arches on each side, working from above down, and removing them so as to expose the spinal cord and the nerve-roots. The dorsal roots are distinguished both by their position and by the ganglia through which they pass; they are especially large and long in the lumbo-sacral region. Cut them in this region on one side of the body.

1. Tetanise the skin of the corresponding foot. No reflex movement is produced: although, if the skin of the opposite foot be stimulated, strong movements are produced in both limbs.

2. Stimulate the distal end of one or more of the cut roots. If care be taken that the current does not spread to a ventral root, no movement results.

3. Stimulate the proximal end. Strong reflex movements are caused. Now cut the ventral roots on the same side in the same region. Notice that on cutting them the leg muscles contract.

4. Stimulate the peripheral end of one or more of the cut ventral roots. There is strong contraction of muscles of the corresponding limb.

5. Stimulate the central end of the same. No effect is observed.

The excitation used for the roots may be mechanical, such as a pinch or snip of the scissors near the cut end. In this case errors which with electrical stimulus may arise from spread of current are obviated. But if the Helmholtz arrangement is used, and only weak induction shocks employed, the risk of spread is much reduced.

CHAPTER XXVII

Reflex Action: Reaction Time

A FROG, the brain of which has been removed,¹ is used for the following experiments. Note the position of the animal when placed on the table, and the absence of spontaneous movements. Suspend the preparation by the lower jaw (Fig. 85). Have ready a large jar or beaker of water (*a*), a small beaker of 2 per 1,000 sulphuric acid (*b*),

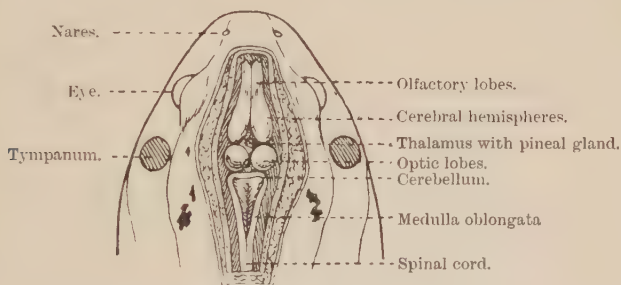


FIG. 84.—Brain of frog *in situ*, exposed by removing the roof of the cranium.

and some small pieces—about 2 mm. square—of filter paper, moistened with 5 per cent. acetic acid. A watch, with seconds hand, or a metronome is also required.

Effect of strength of stimulus.—Gently pinch the toe of one foot with forceps; the leg is drawn up. When again quiescent, pinch the toe more firmly; not only the one pinched, but both legs are

¹ For some of the experiments on reflex action the whole contents of the skull are destroyed. This can be done without hemorrhage by inserting a sharp-pointed plug of wood through the occipital foramen. For other experiments only the cerebrum or brain proper is destroyed, the optic lobes and medulla oblongata being left. This is effected either by crushing the anterior part of the skull with Spencer Wells forceps; or by opening the skull and removing the hemispheres in an anæsthetised animal; or by cutting away all the part of the skull in front of the tympanic membranes with a razor. It is best to perform the operation of destroying the brain or removing the cerebral hemispheres some hours before the experiments on reflex action are to be tried, in order to eliminate the effects of the immediate shock of the operation.

drawn up, and there may also be a movement of the upper limbs (*spread of excitation in cord*).

Effect of summation of stimuli.—Stimulate the toe (1) with single and (2) with a succession of interrupted induced shocks. Weak stimuli only need be used. Determine and note down at what distance of the secondary coil from the primary the reflex response is elicited in each case.

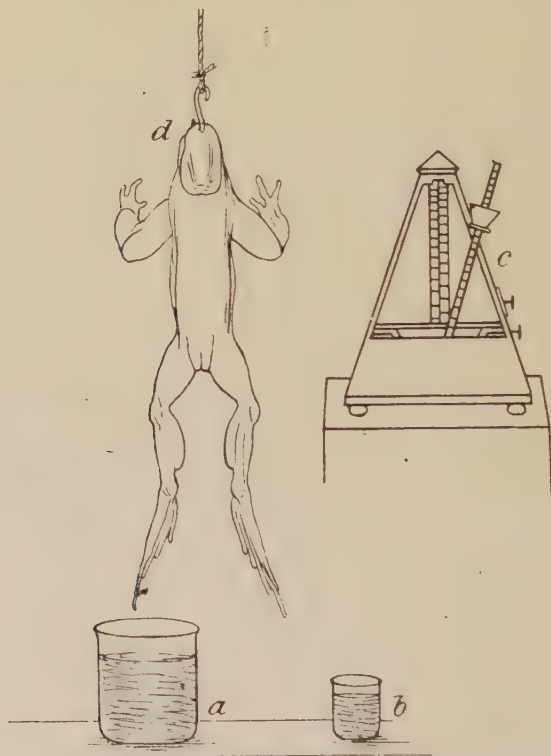


FIG. 85.—Türck's method of determining time of reflex to acid-stimulus applied to toes of decapitated frog. *a*, beaker of water; *b*, beaker of dilute acid; *c*, metronome; *d*, hook suspending frog by lower jaw.

Purposeful reflex action.—Place on one flank a piece of paper moistened with acetic acid; the foot of the same side is raised to rub off the irritant: if that foot is held down, the other foot may be used.

After the observation do not leave the acid in contact with the flank, but wash it off by bringing a large beaker of water up over the legs and lower part of the trunk. The experiment may be repeated upon other places; *e.g.*, the inside of one thigh, the upper part of the

body, and the abdomen, always washing the acid away after each observation.

Time of reflex response; Türck's method.—Having allowed the frog to become quiescent, allow the extremity of the toes to dip into a small beaker of dilute sulphuric acid (2 per 1,000). Count the time in seconds which elapses between the application of the acid and the withdrawal of the toe. Wash the acid off immediately after the withdrawal. Repeat this observation three times at intervals of a few minutes; calculate and record the average time of response.

Inhibition of reflex; Setschenow's experiment.—Place a crystal of salt upon the optic lobes (or on the upper cut end of the cord if the whole brain has been removed), and again determine the time of response after application of dilute sulphuric acid to the toes.

Reflex inhibition of heart.—Fix a decerebrate frog securely on its back upon the frog-cork; expose the heart sufficiently for its beats to be observed. Tap the abdomen smartly with some small heavy instrument, such as the handle of a knife. The effect will be to produce a slowing or complete stoppage of the heart, which will, however, soon recommence beating. The same result is obtained if the abdomen is opened and a loop of intestine strongly stimulated by faradisation.

For this experiment the medulla oblongata must be left.

Effect of drugs on reflex action.—Inject a very small dose of strychnine nitrate (1 drop of a 1 per 1,000 solution) under the skin of a decerebrate frog, and wait for a few minutes until it is absorbed into and distributed by the circulation. It will be found that pinching the skin eventually produces not simple purposeful reflex actions, but convulsive contractions of all the muscles in the body.

Inject a few drops of a 2 per cent. bromide of potassium solution under the skin of another decerebrate frog and determine the reflex time in the same way before and after administration of the drug. It will be found to be much prolonged, or no reflex reaction at all may be visible.

Tendon-reflex; knee-jerk.—In a subject seated in a chair with one leg crossed over the other, or seated on a table with the legs dangling, strike the patellar tendon with the handle of a knife or the back of a thin book. Notice the sudden jerk forward of the leg owing to the contraction of the vastus internus. This can be recorded by a transmission myograph (see p. 44).

Reinforcement of tendon-reflex.—Just before striking the patellar tendon cause the subject to clench his fist. The movement of the leg will be stronger, or will be elicited with a slighter tap on the tendon.

Reflex action in mammals.—The reflex actions of mammals can be studied in decerebrated or decapitated preparations (see Sherrington's *Mammalian Physiology*), reflexes being elicited in various ways, as by touching or pricking an ear or a paw or the skin of the flank or the side of the thorax, or by imparting passive movements (changes of posture) to the head. If records are taken both from the muscles concerned in producing the reflex movement and from the antagonistic muscles, it will be seen that any tonic contraction which the latter may be exhibiting is lessened or inhibited. Tendon-reflexes, such as the

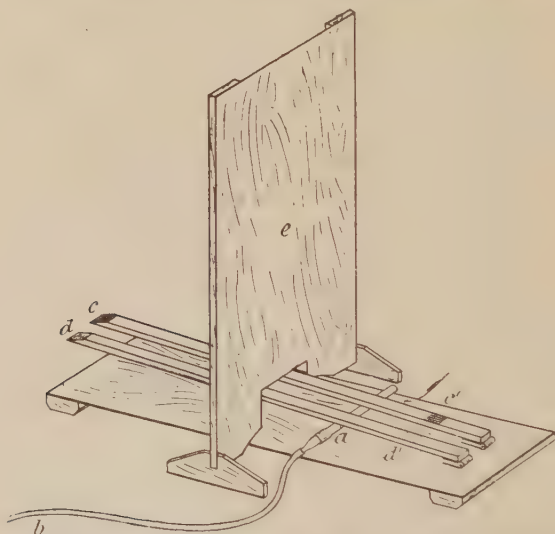


FIG. 86.—Waller's apparatus for reaction time. *a*, rubber tube closed at one end and at the other connected by *b* with a tambour (not shown); *c*, *c'*, *d*, *d'*, levers (with coloured patches) hinged near *c'*, *d'*, and resting on the rubber tube, *a*; *e*, wooden screen. (The tube, *a*, should be placed on the other side of the screen.)

knee-jerk (see above) and the ankle-clonus, obtained by forcibly bending the foot at the ankle, can also be well observed in such a preparation.

Reaction time in man.—The reaction time in man may be determined by an arrangement of electric signals, but is done more simply by Waller's apparatus (Fig. 86). This consists of two wooden levers lying across a piece of india-rubber tube. One end of this is closed; the other is connected with a tambour which writes upon a drum, the speed of which should be moderate. A screen hides the movements of the experimenter from the person experimented on, who sits at the table with one finger resting lightly on the

extremity of one of the levers. He is to respond by pressing the lever the instant he (1) feels a movement of that lever, his eyes being shut; (2) hears a tap on the second lever; (3) sees a movement which is imparted to the second lever by the experimenter, who presses it down on the other side of the screen. In each case two marks are recorded upon the abscissa: one being that which is made by the experimenter in imparting the stimulus, and the other that made by the observed person in responding. The interval between the two marks, which can be measured by the aid of a time tracing, indicates the time between stimulus and response—i.e., the reaction time—in the case of each of the three senses. To determine this with any accuracy several observations must be made with each method of stimulation and the shortest time taken.

Discrimination time.—For the measurement of this the observed person places one finger over each lever. It is agreed beforehand that he is only to react to a stimulus received on the one side, not on the other. Or it may be agreed that it is only the hand on the side which receives the stimulus which is to be used for the response. The experimenter may stimulate either. It will be found that the reaction time is lengthened by a certain interval, and this increase of reaction time is termed the *discrimination time*.]

Variations of the above experiments can be made by the employment of different sounds and exhibition of different colours, but the methods for recording the reaction times are essentially the same. For rapid and accurate work it is usual to employ a specially constructed clock or other apparatus which can register the time of a reaction to a small fraction of a second.

Excitation of the cortex cerebri.—A monkey, anaesthetised with ether, is best used for this demonstration. A considerable portion of the skull cap is removed on one side by trephining the skull and enlarging the aperture by bone-forceps. The dura mater is then cut through below and reflected towards the middle line, thus exposing the cerebral surface. A pair of blunt-pointed platinum electrodes, with their points 1 mm. apart, is connected with a key in the secondary circuit of an induction coil (use the Helmholtz modification) and is applied to various spots in the excitable region of the frontal lobe, to the first temporal gyrus and to the occipital lobe, and the results are noted.

The monopolar method of stimulation may also be employed for these observations (Sherrington). In this case one electrode is a flat pad of wash-leather wetted with strong salt solution and laid on any part of the body (the skin should first be shaved); the other [stimulating] electrode is a small spiral platinum wire with blunt point, which is applied to the excitable areas of the cortex.

CHAPTER XXVIII

Cutaneous Sensations

Cutaneous sensations. Pain spots.—Explore with a sharp pin or needle a portion of the skin of the palmar aspect of the forearm of another person (who should keep his eyes closed, or look away), pressing the point firmly here and there, but without penetrating the surface. Notice that whereas at some places the prick is painful, at others no pain is caused, the feeling being either one of touch or of pressure. For gauging the amount of pressure of the needle which is needed to elicit a definite sensation of pain, an instrument termed the algesimeter is employed, the pressure being produced by compression of a spiral spring, and the amount in grammes indicated on a dial.

Warmth spots.—Substitute for the pin a thick copper rod with a smooth, blunt point; the rod may be provided with a cork handle. Warm the rod by immersing it in water heated to 45° C. Explore the skin by passing the point of the rod slowly over it. It will be found that the sensation is one of warmth only at certain points, where it is very distinct; at others it is merely a sensation of touch.

Cold spots.—Repeat with the same or a similar rod cooled by immersion in ice-cold water. In this way spots sensitive to cold alone flash out on passing the point slowly over the surface of the skin: they are not the same as those which are sensitive to warmth.

The various spots may be mapped out upon a patch of the skin with coloured inks or pencils, and may be tested again later. According to most observers they are constant in position.

Touch sensations: Determination of the relative delicacy of different parts to touch.—Take a fine bristle or coarse hair 2 inches long, and fix it with sealing-wax to a match to serve as a holder (Fig. 87). Explore in another person (who is not to see the part which is touched) any part of the skin, determining the spots which are most sensitive to the pressure of the hair. The point of this is to be brought vertically on the skin without lateral movement and pressed down only just enough to bend it slightly. By using a number of bristles of different thickness a certain rough scale of delicacy of touch on different parts of the body

can be made out. Notice that the slightest side-movement greatly increases the sensitiveness of any part to the touch, especially if hairs are deflected. This can also be shown with a scrap of cotton-wool, the touch of which may be imperceptible until it is moved.

The series of bristles just described form collectively v. Frey's *æsthesiometer*.

A more elaborate *æsthesiometer* on v. Frey's principle may be employed in which a bristle is made to protrude from the end of a fine tube to a variable extent, which can be exactly measured. The longer the part protruding the more easily is the bristle bent on pressure. Bristles of different diameter can be used. The delicacy of touch is gauged according to the length of the protruding part, which is just felt as touch when pressed upon the surface of the skin until it bends over.



FIG. 87.—v. Frey's hair *æsthesiometer*.

Graham Brown's *æsthesiometer* consists of a convex piece of steel with a polished surface, a part of which can be made to project beyond the rest by turning a truly cut micrometer screw. The relative delicacy of touch is gauged by the power of feeling different degrees of projection. This is especially applicable to the lips or to the palmar surfaces of the finger-tips.

Discrimination of two points.—For this purpose a pair of compasses with blunted ivory points is used ; their distance apart is measured upon a scale after each observation. Or the points may be permanently connected with the scale, one being fixed at its zero and the other sliding along it (Sieveking's *æsthesiometer*). Test in this manner in another person various parts of the integument (back and front of arm, fingers, lips, tip of tongue, etc.) and record the distances at which the two points are discriminated as separate, causing them always to be applied simultaneously, and without lateral movement.

Accuracy of localisation.—This is investigated by lightly touching any part of the skin and immediately causing the subject to place his finger upon the part touched.

In all the above experiments the subject should be blindfolded.

CHAPTER XXIX

Experiments on the Dioptric Mechanism

Dissection.—An eye (ox, sheep, or pig) is to be dissected. (1) After cleaning away from the globe all remains of muscles, fat, etc., cut a window out from the back, removing the sclera and choroid and exposing the retina. Notice that when the cornea is turned to the window an inverted image of this is formed upon the retina. (2) Cut away a small portion of the sclera at the edge of the cornea. A grey-looking ring of plain muscular tissue is exposed, the fibres passing from the corneo-sclerotic junction backwards over and into the choroid. This is the ciliary muscle. (3) Cut the eye in two at its equator. Notice, in the posterior half, from which the jelly-like vitreous humour flows away, the retina—usually somewhat opaque and crumpled after death—spreading out from the entrance of the optic nerve: in the anterior half the lens within its capsule, the suspensory ligament around the margin of the lens, the radiating ciliary processes. (4) Snip through the suspensory ligament all round the lens, which can be removed within its capsule; the iris is now seen projecting into the anterior chamber.

Accommodation; Change in shape of the lens.—That the lens bulges forward in accommodation is shown in various ways.

1. Stand at the side of another person and let him fix his vision on a distant object, looking beyond a near object such as a needle or pencil held a few inches from the eye. Notice his iris, which can be seen through the edge of the cornea lying against the front of the lens. Now let the subject look at the near object. His iris is seen to advance, being pushed forwards by the bulging lens; the pupil at the same time contracts.

2. *Nanson's images.*—In a dark room hold a candle at one side of the eye of a subject, and, standing on the other side, observe the reflected images—a bright one from the front of the cornea, a less bright one from the front of the lens, and a duller, small, and inverted image—difficult to see—from the back of the lens. The subject as before is to have his vision fixed at first on a distant object, and is then to transfer his gaze to a near object in the same line. The

image reflected from the front of the lens becomes smaller and moves nearer to that reflected from the front of the cornea; the other images remain unaltered. This change of the second image is due to bulging of the anterior surface of the lens.

3. *Phakoscope*.—The same experiment may be performed with a phakoscope (Fig. 88) with less trouble, since all the points are fixed. The instrument—a triangular box with truncated angles *a*, *b*, *c*—is used in a darkened room. A lamp is placed in such a position that the light from the two square window prisms at *c* falls upon the observed eye at *a*. The observer looks through the opening at *b* and sees in the observed eye three pairs of images—two bright squares (reflected from the anterior surface of the cornea), two larger but less distinct squares, and two smaller and much dimmer squares. The two last pairs, being reflected from the anterior and posterior surfaces of the lens respectively, can, of course, only be seen within the pupil. The last pair is difficult to make out. If the subject is asked, first to look *past* the needle *n* at a distant window, and then *at* the needle, the middle double image becomes smaller and slightly brighter during accommodation for the near object; the squares approaching each other and coming nearer to the corneal image; the other two double images remain unaffected.

Near and far points of distinct vision.—A wooden scale about 12 inches long is marked in inches or centimetres. One end of this is placed close to the eye, and a needle is put in about 5 inches off. If the eye is normal, the needle should be seen sharply at this distance and at any point beyond; but if it is brought nearer the eye its image becomes blurred. If the eye is myopic the needle may be brought nearer than 5 inches without its image being blurred; when blurring occurs the near point for that eye has been passed.

If the eye is hypermetropic the needle will already appear blurred at 5 inches, and it may be required to be moved considerably further from the eye before the near point of distinct vision is passed.

Pater Scheiner's experiment.—The observation is rendered easier

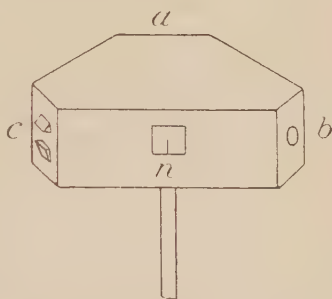


FIG. 88.—Phakoscope: *a*, situation of observed eye; *b*, ditto of observer's eye; *c*, lenses; *n*, aperture with needle.

and more striking by Scheiner's device of observing the needle through two pinholes made close to one another and side by side in a card fixed vertically at one end of the scale (Fig. 89). In this case, when the needle is nearer to or further from the near or far points of distinct vision, its image appears not blurred but double.

That the eye cannot simultaneously obtain sharp images of a near and a distant object is shown by taking two needles and fixing one at about 5 inches along the scale and the other some inches further. If now, in Scheiner's experiment, the eye is focused on the near needle, the far one looks double, and *vice versa*.

Changes in the pupil produced by drugs.¹—Carefully enucleate the eyeballs of a frog which has just been killed and place each in

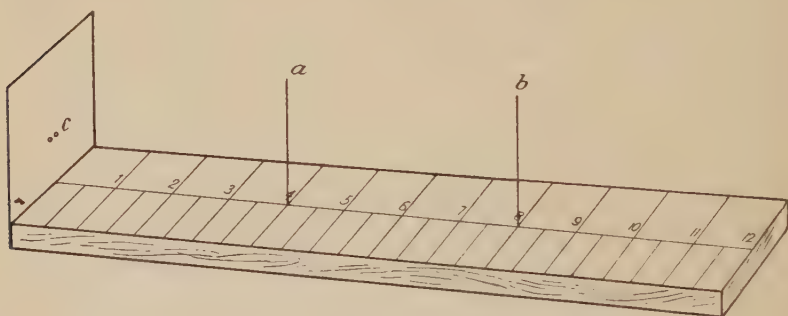


FIG. 89.—Board with perforated card for Scheiner's experiment. *a, b*, needles; *c*, perforations in card.

a watch-glass of Ringer's solution. Measure the diameter of the pupils with compasses and note down the size of each. Add to the contents of one watch glass a drop of extract of suprarenal capsule or of 1 in 1,000 adrenaline solution. After a short time again measure the pupils. Repeat the measurement after an hour or more. Dilute solutions of eserine and of atropine can be similarly tested.

The effects of drugs are also investigated, in man or animals, by dropping them on the conjunctiva, and, in animals, by injecting them into a vein.

The Ophthalmoscope.—*Direct method.*—The instrument which is used for examining the interior of the eyeball consists essentially of a small concave mirror with a hole in the centre. Practise first on an artificial model of the eye and then on the living subject. [It can be practised upon a rabbit: a drop or two of a 1 per cent.

¹ The effects upon the pupil of cutting and stimulating the sympathetic have already been studied (see p. 99).

solution of atropine should previously be instilled into the eye. Or a frog, with the body wrapped in a cloth, may be employed.] Only a limited part of the retina is seen at one time, but it is much magnified.

The subject is seated in a darkened room with a light, not too bright, near his ear. The observer sits in front of, and on a slightly higher level than, the subject, close to him. The observer holds the mirror in front of and close to his own (corresponding) eye, and, throwing the beam of light into the subject's eye, asks him to look upwards and inwards. The observer then moves the mirror, with his eye close behind it, backwards and forwards, looking through the hole in the centre, and when the proper distance is found (2 to 3 inches), the retina comes into view with its vessels running in different directions on a red ground. The mirror is moved about until the optic disc (entrance of optic nerve) is seen as a whitish circular area with the central artery and vein of the retina emerging at its centre. The image of the fundus is virtual (erect), and is enlarged because the refracting surfaces of the subject's eye magnify the parts under observation.

Indirect method.—With the subject as before, the observer places himself about 18 inches in front of the patient and throws the light on the pupil as in the direct method. He then takes a small biconvex lens (2 to 3 inches focus) in his left hand, and, holding it vertically between the thumb and forefinger at a distance of 2 to 3 inches from the patient's eye, moves his own eye with the mirror in front of it backwards and forwards and from side to side until the optic disc and other parts of the retina are seen. The image is real (inverted), and is only slightly magnified.

Retinoscopy is difficult in the human subject unless the pupil has been previously dilated by atropine. If either the patient or observer has abnormal vision this is corrected by suitable lenses placed behind the aperture in the mirror.

Entoptic appearances of the lens and vitreous humor.—By a series of very simple experiments the student will be able to see certain details of the structure of the lens, vitreous humor, and retinal vessels of his own eye.

If a small source of light is looked at through a strong biconcave lens (-16 diopters) held about 50 cm. from the eye, the light source will be seen as an almost circular spot of light, surrounded by a serrated margin. This serrated margin is produced by the margin of the iris of the observer's own eye, while the bright spot of light corresponds to the pupil. If the other eye is illuminated, the pupil can be seen to contract. When the biconcave lens is brought still

nearer the eye, irregular fibre-like markings can be seen in the spot of light which corresponds to the pupil; these markings are caused by the fibres of the lens. If the biconcave lens is approached to within a few centimeters of the eye, the markings disappear and become replaced by irregularly moving spots; these are due to floating cells in the anterior part of the vitreous.

Instead of a biconcave lens, an ordinary microscope, the field of which is evenly illuminated, may be used. The observer looks into the eyepiece from a distance of about 20 cm.; under these circumstances he will see in the eyepiece the pupil as a circular spot of light, surrounded by the serrated margin of the iris. As the eye of the observer is brought nearer to the eyepiece the spot of light becomes larger until, at a point about 5 cm. away, the fibre-like structure of the lens appears. If the eye is brought still closer, vitreous "floaters" can be seen moving across the illuminated field.

The part of the vitreous lying immediately in front of the retina can be inspected by looking at an evenly illuminated surface, such as a bright but cloudy sky. Numerous irregular spots and threads will appear moving across the field of vision; these are due to tissue elements in the vitreous humor. They are the well known *muscae volitantes*.

CHAPTER XXX

Stimulation of the Retina

Electrical changes.—That an electrical change results from the action of light upon the retina can be shown in the frog. The eye is enucleated and is placed on non-polarisable electrodes, one of which is in contact with the cut optic nerve, and the other with the front of the eye. The electrodes are connected with a galvanometer (or electrometer) (see Chapter XIII.), and the preparation is placed in a dark box. On letting light into the box an electric change is produced in the retina, and the galvanometer or electrometer is deflected. On removing the light there is another deflection in the same direction.

Blind spot ; Mariotte's experiment.—Make a mark of any sort (such as a cross) upon a piece of paper, and fix one eye—say the right—upon it, closing the other eye and placing the head about 6 inches from the paper. It will be found that over a considerable area of irregular shape, about 3 or $3\frac{1}{2}$ inches from the cross, the point of a pen or pencil will not be visible because its image falls upon the place where the optic nerve enters the retina. Even a large black dot made in this area upon the white paper is quite invisible as long as the eye is fixed upon the cross. The experiment shows that the optic nerve fibres are insensitive to light. Map out the blind area, noting distance of eye from paper.

Macula lutea ; Maxwell's experiment.—Close the eyes for a minute ; then, opening one of them, hold a bottle with parallel sides containing a solution of chrome-alum—which has a greenish colour—between the eye and a uniform source of light such as a white cloud. The middle of the field of vision will be occupied by an oval rose-coloured area ; the alteration in colour of this part is due to absorption by the yellowish pigment of the macula of some of the rays transmitted through the chrome-alum ; which is dichroic, transmitting greenish-blue and red rays : the former are absorbed.

Purkinje's experiment.—This is to be attempted in a darkened room. Stand about 8 feet from a sheet of white or grey paper fixed to the wall and get an assistant to illuminate the retina through the sclerotic by means of a converging lens and lamp or candle held at

one side of the eye. Look steadily at the paper with one eye, accommodating for distance. In a minute or two a number of branching figures will be seen like the roots of trees. These are the shadows of the retinal blood-vessels. When the light is moved the shadows are also seen to move. This experiment shows that the receptive visual cells lie behind the blood-vessels of the retina. The presence of the vessels may also be appreciated by moving the field in relation to the retina. Look at the sky through a pinhole in a sheet of cardboard, give the card an up and down, side to side, and lastly a rotatory motion, and the branching shadows will be perceived with a central free space corresponding to the macula.

The retinal vessels can still better be seen by using a very small electric bulb mounted on a stem. The bulb is pressed directly backwards on the lower eyelid of the closed eye, and moved about slightly; in a certain position, which has to be found by trial, the observer will see his own retinal vessels standing out as red streaks on a darker red ground. The vessels disappear into a dark area, the blind spot. In carrying out this experiment it is best to close both eyes.

The red corpuscles moving in the retinal vessels can be seen by looking at a bright sky through a piece of dark-blue glass. After a few seconds the field of vision exhibits minute silvery spots in rapid movement; these are caused by the shadows of the red corpuscles within the retinal vessels falling on the light-sensitive rods and cones.

Perimetry.—The perimeter is an instrument for testing and recording light perceptions in different parts of the retina. The eye is fixed upon a point in the centre of the concave hemisphere forming the perimeter, and a white disc is brought gradually from the edge of the hemisphere nearer and nearer to the centre until it is perceived. This is repeated along different meridians, and the results are marked on a chart at the back of the instrument. By using coloured discs instead of white the area of the retina which is sensitive to each colour can also be ascertained.

Testing for colour vision. Edridge-Green's lamp and spectroscope. Holmgren's wools.—The best practical method for testing colour vision is by the use of a lamp provided with glasses of different colour, the subject being expected to name the colour which is exhibited. A more accurate method of obtaining spectral colours for testing purposes is the employment of a spectroscope so arranged that only a definite part of the spectrum with a pure spectral colour is visible at one time.

A method which has been considerably used for testing colour vision is to take a box full of skeins of wool dyed with different colours, and, selecting one skein, to ask the person who is being tested to pick

out any that match it. If he is colour-blind he is liable to make serious mistakes, matching grey with red, green with grey or red, and so on ; but it occasionally happens that persons who fail completely with the lamp test are able, probably by judging from the intensity of the reflected light, to match the Holmgren wools fairly well.

Successive contrast.—Fix the vision upon a white spot on a dark ground. After one minute look at a uniform white surface such as a white ceiling. A dark spot now occupies the centre of the field of vision.

This experiment is varied by employing colours—*e.g.*, a yellow spot on a blue ground or *vice versa* ; and a red spot on a green ground or *vice versa*. In each case the vision is transferred to a uniform white surface and the contrast colours are observed.

For the grounds, coloured paper is used ; for the spots, either paper discs or wafers.

Meyer's experiment.—Place a grey disc upon a yellow ground, and cover the whole with thin tissue paper : the grey disc at once appears blue ; the contrast colour of the yellow. If a blue ground be used the disc will appear yellow. The same experiment may be repeated with red and green grounds. On the white ground the grey disc will appear darker ; on a black ground lighter.

Colour mixer.—This usually takes the form of a revolving circular plate on which sectors of different coloured cards can be arranged. Owing to the fact that retinal impressions have an appreciable duration, the colours appear blended during the revolution of the plate, and the mixing of the colours on the retina can thus be studied.

Stereoscope.—The fact that in stereoscopic vision the mind combines the effects produced by slightly dissimilar pictures falling on the two retinae is illustrated by the ordinary stereoscope.

Persistence of visual impressions.—The fact that a visual impression persists for a brief interval after removal of the stimulus is shown by the apparent luminous line described in the air by rapidly moving the glowing end of a burnt stick. It is also familiarly illustrated by cinematograph pictures.

CHAPTER XXXI

The Production of Vocal Sounds. Analysis of Sounds. Audition. Semicircular Canals

Use of the laryngoscope.—The laryngoscope consists of a small circular plane mirror fixed to a handle at a suitable angle; a large concave mirror with a hole in the centre is strapped to the operator's forehead.

Method of procedure.—Practise first on an artificial model of the larynx and afterwards on the living subject. The latter is placed on a stool with a lamp over his right shoulder, a little above the level of his mouth. The observer sits opposite and close to the subject with the large mirror attached to his forehead. The subject is asked to open his mouth, incline his head slightly backwards, protrude his tongue, and hold it down with a handkerchief. The observer manoeuvres his head until the back of the subject's throat is brightly illuminated; he then takes the small mirror in his right hand, warms it slightly in a flame to prevent moisture condensing on its surface (the back of the mirror should be just perceptibly warm to the cheek), and, holding the handle as one does a pen, pushes it horizontally backwards until it touches the uvula. First the dorsum of the tongue is seen in the mirror, then, as the handle is depressed, the epiglottis; then the glottis and vocal cords come into view. The image of the larynx thus obtained is an inverted one. In ordinary breathing the glottis is open; if the patient is asked to sound a high note the vocal cords may be seen to come together and to vibrate, and if he is asked to take a deep breath they separate; the interior of the trachea and even its bifurcation may then be seen through the widely open glottis.

Any tendency to retch when the mirror comes in contact with the soft palate may be diminished by the application of a solution of cocaine to the mucous membrane.

The movements of the laryngeal cartilages are studied in a model which represents them articulated together. The action of the muscles can be imitated by threads, and the vocal cords by thin flat rubber bands stretched between the thyroid and arytenoids.

The production of vowel sounds.—Notice that the production of the vowel sounds (*ah*, *eh*, *ee*, *o*, *oo*) is accompanied by changes in the

shape and size of the resonating chamber formed by the throat and buccal cavity.

The production of consonants.—Notice that most of the consonants are produced by an interruption, complete or incomplete, of the blast of air which is producing the vibration of the vocal cords, the interruption occurring either at the back of the palate (gutturals), at the front of the palate (linguals), or at the lips (labials). Notice also that the character of the interruption is a factor in determining the quality of the consonant: thus, with some, such as *k*, *b*, and *t*, it is sudden or explosive; with others, such as *m* and *n*, the nasal cavities are brought in as resonators; with others, such as *ch*, *f*, and *s*, the blast is continuous, but is made to traverse a narrowed part of the cavity: whilst with *qu* there is an actual vibration of the narrowed part.

The production of sounds by vibration of the vocal cords, and the dependence of the pitch of sounds on the tension of the cords.—Take a sheep's larynx and tie a glass tube into the trachea. Fix the larynx securely on a board, with the dorsal surface downwards, by wires or strong pins through the cricoid cartilage and epiglottis. Pass a string through the lower part of the thyroid cartilage. When this string is pulled vertically upwards, the vocal cords are stretched in proportion to the pull, and become approximated. If air is blown through the tube in the trachea, the edges of the cords are set in vibration when thus approximated and a sound is emitted, the pitch of which varies with the tension of the cords. The blast of air should be of the same strength throughout.

Analysis of sounds of musical instruments and of the voice.—The analysis can be made by applying different Helmholtz resonators to the ear of the observer. König's manometric flames, which are provided with these resonators and are examined with the aid of vertical rotating mirrors, are also employed for this purpose.

Determination of range of pitch for audition.—The highest and lowest notes which can be appreciated are determined by the use of Galton's adjustable whistle.

Conduction of sound by the bones of the skull.—Stop the ears with wool. Set a small tuning-fork in vibration, and hold it with the base touching the top of the skull. The sound is propagated to the cochlea by the bones of the skull.

Inspection of the tympanic membrane.—Using a mirror with a central aperture fixed in front of the eye, throw the reflection of a lamp into the meatus of the subject, whose external ear must be drawn somewhat backwards and upwards.

Propagation of sound to the internal ear.—The mode of transmission may be studied with the aid of a model showing the bones of the

middle ear and their attachments to the membrana tympani and the fenestra ovalis. The model shows that when the tympanic membrane—to which the handle of the malleus is attached—is pressed inwards, the base of the stapes, which fits into the fenestra ovalis, follows the movement; but when the tympanic membrane is forced outwards beyond a certain point the stapes is not dragged after it, owing to the nature of the articulation between malleus and incus. The model also shows the effect of the tensor tympani in pulling inwards the handle of the malleus and with it the membrana tympani, and the effect of the stapedius in pulling the head of the stapes backwards and causing the base to be tilted within the fenestra ovalis, thus rendering tight the ligament which fixes it in that aperture.

Semicircular canals.—For demonstrating the effects of injury to semicircular canals, a bird (pigeon) is employed. An opening is made in the side of the skull of the anaesthetised animal with a very small trephine, and through the aperture a special instrument is introduced and passed underneath the dura mater until one of the bony semicircular canals (which in the bird project above the surface of the petrous bone) is met with; the canal can then be broken across.

For observing the effects of stimulation of the canals in man a strong galvanic current is passed from one side of the head to the other, pad electrodes wetted with strong salt solution being applied in the neighbourhood of the ears. The stimulation occurs on the side of the kathode.

The effects of stimulating the nerve-terminations in the ampullæ of the semicircular canals by movements of the endolymph are studied by the aid of a turn-table, upon which the subject (blindfolded) is seated. The several canals are affected according to the inclination of the head—the external when the head is erect, the superior with the head inclined forwards, the posterior with the head inclined laterally. On ceasing the rotation varying movements of the body and eyes are produced, involuntary in character and accompanied by giddiness.

The effects of passively changing the posture of the head upon the position of the limbs can be studied in an animal (cat) decerebrated by Sherrington's method (see *Mammalian Physiology*) and suspended by a broad bandage round the trunk. These effects are due to stimulation of the nerves of the labyrinth (utricle, saccule) by pressure of the otoliths.

CHAPTER XXXII

Taste and Smell

Taste.—(a) To test the localisation of taste, direct the subject to close his eyes and put out his tongue. This organ is then dried, and different parts are touched with a small brush or a glass rod moistened with the sapid substance in solution. After each observation the mouth must be rinsed with water. The following solutions may be used for testing the four qualities of taste, viz.: for *bitter*, 1 per cent. solution of quinine sulphate; for *sweet*, 5 per cent. solution of sugar; for *acid*, 2 per cent. solution of citric acid; and for *salt*, 5 per cent. solution of common salt. Notice the time which intervenes between the application of the sapid substance and its effect. Record your results as regards localisation upon an outline plan of the tongue.

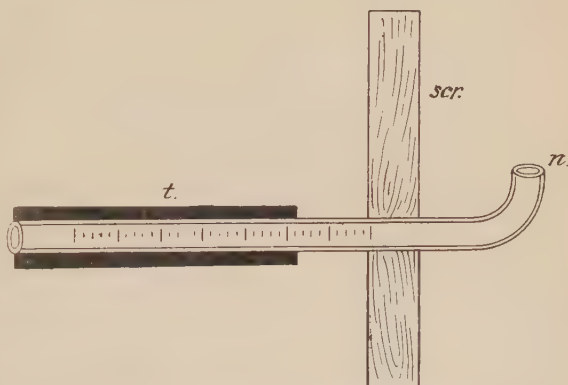


FIG. 90.—Zwaardemaker's olfactometer. *n*, nose-piece; *scr*, screen; *t*, porous tube sliding over graduated glass tube.

(b) Test different parts of the tongue by applying closely-set electrodes arranged to conduct a weak faradising current.

(c) Chew a leaf of *Gymnema sylvestris*, or paint the tongue with cocaine solution, and determine whether the taste of any of the varieties of sapid substances is affected.

Smell.—The sense of smell is tested by Zwaardemaker's olfactometer, which consists of a glass tube with one end adapted to the nostril, while over the other end a tube, which can be impregnated with the odoriferous substance, slides, so that a greater or less amount of its inner surface is exposed to the air which is passing through the glass tube into the nostril (Fig. 90).

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